Taiwania 62(3): 283-293, 2017
DOI: 10.6165/tai.2017.62.283

Recruitment dynamics mediated by ungulate herbivory can affect species coexistence for tree seedlings assemblages

Chi-Yu WENG[1], Chih-hao HSIEH[1,2,3,4,5], and Mong-Huai SU[6,*]

1. Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617, Taiwan.
2. Institute of Oceanography, National Taiwan University, Taipei 10617, Taiwan.
3. Research Center for Environmental Changes, Academia Sinica, Taipei 11529, Taiwan.
4. Department of Life Science, National Taiwan University, Taipei 10617, Taiwan.
5. National Center for Theoretical Sciences, Taipei 10617, Taiwan.
6. Department of Forestry and Nature Conservation, Chinese Culture University, Taiwan.
[*] Corresponding author's email: smh2@faculty.pccu.edu.tw

(Manuscript received 2 March 2017; accepted 12 June 2017; online published 19 July 2017)

ABSTRACT: The best-known mechanism that herbivory affects species coexistence of tree seedlings is negative density-dependency driven by specialist natural enemies. However, in a forest with intense herbivory by non-specialists, what causes a diversifying seedling bank if rare species do not benefit from negative density-dependency in dominant species? We hypothesize that generalist herbivores can cause unevenly distributed species-specific mortality, which mediates recruitment dynamics and therefore affects species coexistence. To answer this question, we conducted a fence-control experiment in a montane cloud forest, Taiwan, and found that herbivorous damages were mainly caused by ungulates, which are generalists. We explored ungulate herbivory effects on recruitment dynamics by censusing tree seedling dynamics for three years. We found that herbivorous damages by ungulates significantly cause seedling death, mostly at their early stage of establishment. The percentage of death caused by herbivory varied among species. In particular, nurse plants and seedling initial height help shade-tolerant species to persist under such intense herbivory. Whereas, deaths caused by other factors occurred more often in older seedlings, with a consistent low percentage among species. We then tested species coexistence maintenance by dynamic modelling under different scenarios of ungulate herbivory. Raising percentages of death by herbivory changes relative species abundances by suppressing light-demanding species and increasing shade-tolerant species. Density-dependent mortality immediately after bursts of recruitments can suppress dominance of abundant species. With ungulate herbivory, fluctuating recruitment further prevent rare species from apparent competition induced by abundant species. Such bio-processes can interact with ungulate herbivory so that long-term coexistence can be facilitated.

KEY WORDS: Dynamic modelling, Montane cloud forest, Recruitment dynamics, Seedling, Species coexistence, Ungulate herbivory.

INTRODUCTION

Most studies on recruitment dynamics have tested the Janzen-Connell hypothesis: specialist natural enemies (usually belonging to pathogens or insects) can suppress abundant species through conspecific density-dependent mortality and thus benefit rare species (Dyer *et al*., 2010; Bagchi *et al*., 2014; Comita *et al*., 2014; Norghauer and Newbery, 2014). However, still few researches address mammalian herbivores, especially ungulates, which can effectively mediate recruitment dynamics by herbivory in the understory, and affect species coexistence of tree seedlings (Asquith *et al*., 1997; Royo and Carson, 2005; Smit and Vandenberghe, 2007; Royo *et al*., 2010; Paine *et al*., 2016). Empirical studies on how ungulate herbivory affect seedling species coexistence are rare for two reasons. First, ungulates are more often generalists (mixed feeders with flexible diets by browsing or by grazing) and purely dietary specialization are very rare for their nutritional requirements (Dearing *et al*., 2000). Secondly, ungulate herbivory is usually underestimated because compound causes of death or “vanishing deads” of seedlings due to grazing by ungulates (Hulme, 1996) are not easy to identify or distinguish in field surveys.

Because ungulates are more often generalist herbivores to tree seedlings, knowing how ungulate herbivory affects on seedling survival i.e., either causing species-specific deaths or just random deaths irrespective of species, is prerequisite to explore consequent herbivory effects on species coexistence. In particular, unevenly distributed species-specific deaths can greatly change species assembly in bio-communities (Wright, 2002). Usually, non-random, species-specific deaths occur at early stage of seedling establishment (Green *et al*., 2014); however, over ontogeny, mortality of seedling species is towards random while species richness of the survivors become higher. These imply that a positive consequence for species coexistence can arise from species-specific seedling deaths at early stage. Species-specific deaths of new recruits or younger seedlings may be caused by some selective browsers (Royo *et al*., 2010; Curran and Webb, 2011); however, whether generalists (e.g. mixed feeders or grazers) can cause species-specific deaths for new recruits remains inconclusive. These are in contrast to chance deaths (and also chance births) as suggested in the “community drift model” (Hubbell, 1979), which assumes ecologically equivalence in species and theoretically predicts random processes can drive species coexistence in community dynamics.

The potential of grazer effects of generalists to generate unevenly distributed species-specific deaths of seedlings may be underestimated because their major diets are herbs, but not woody seedlings. However in reality, grazers can reduce exploitative competition from understory plants to seedlings (Hulme, 1996), and thus indirectly benefit shade-tolerant seedling species. In addition, for resisting against grazers and browsers at an early stage of tree seedlings, some species-specific attributes help seedlings to survive after herbivorous damages. For example, tree seedling species with large seeds, hypogeal cotyledons (which will not be raised aboveground after germination), usually with greater initial height, are not easily eaten completely by herbivores. Most importantly, large-seeded seedlings are able to resprout from hypogeal cotyledons that facilitate establishment (Baraloto and Forget, 2007). In contrast, epigeal, small-seeded tree seedlings, usually light-demanding species, are easily become “vanishing deads” when suffering herbivory. Furthermore, shade-tolerant seedling species can benefit from neighboring understory plants or shrubs that provide nurse-plant effects, which may create shelter for smaller seedlings to grow underneath them and reduce ungulate herbivory (George and Bazzaz, 1999; Royo and Carson, 2008).

Species-specific deaths by ungulate herbivory can be the consequences through bio-interactions (e.g., nurse-plant effects) or species attributes (e.g., shade-tolerance, seed size) that help to resist ungulate herbivory. However, whether this species-specific effect on seedlings can be beneficial for rare seedling species remains unclear. For this argument, the well-proven mechanism of density-dependent deaths (Comita *et al*., 2014) is still worth rethinking even if considering that ungulates are non-specialists to tree seedlings. Actually for insect-herbivores, a generalists-removal-experiment resulted in increased seedling species richness, as well as increased abundances of rare species (Dyer *et al*., 2010). For generalist enemies to seedlings, apparent competition further hinders species coexistence. Apparent competition means that prey species may indirectly depress each other under increment of shared natural enemies (Holt, 1977); for tree seedlings, apparent competition is more likely to happen when sizeable proportion of recruitments of different species simultaneously burst in time (hereafter, synchronized recruitments). Under this circumstance, rare seedling species may be impacted by apparent competition resulted from nearby abundant seedling species that attract ungulates’ browsing. A possible mechanism that can prevent rare seedling species from apparent competition is a lottery model through recruitment fluctuations (Hulme, 1996). Aperiodic recruitment fluctuations by long-lived tree species increase temporal heterogeneity, thus reduce interspecific competition, and facilitate chance survivors in a long-term process, so called “storage effects” (Usinowicz *et al*., 2012). To explore seedling species coexistence, the mechanisms that can effectively interact with ungulate herbivory from this long-term perspective should be addressed (Lischke and Löffler, 2006; Usinowicz *et al*., 2012; Green *et al*., 2014; Paine *et al*., 2016).

In this study, our objective is to explore which factors are important at maintaining a diversifying seedling bank in a forest with frequent herbivory by ungulates. We expected that intense ungulate herbivory would greatly affect seedling survival and growth; as such, species coexistence in seedling bank is likely mediated by ungulate herbivory. We hypothesize that ungulate herbivory can cause unevenly distributed species-specific deaths, and thus change recruitment dynamics and subsequent community assembly. To examine our expectation, we conducted an experiment with fence control to determine whether most of the herbivorous damages were caused by ungulates. We monitored recruitment dynamics for three years and recorded each seedling’s surviving state and causes of death. We evaluated “parameters” concerning recruitment and death of each seedling species based on our field surveys, and used a dynamic model to simulate community assembly “reconstructing” from random shuffling bursts of recruitment and death events. By controlling intensity of herbivory pressure and incorporating bio-processes such as density-dependent effects and recruitment fluctuations, our dynamic model is designated to explore possible mechanisms that ungulate herbivory affects seedling species coexistence in a long-term regeneration process.

MATERIAL and METHODS

Study area

We conducted this study in the Nanhsi forest dynamics plot (23°27'40.7" N, 120°54'22.2" E, 8.37 ha, ranging from 1,960 to 2,060 m elevation) (Yang *et al*., 2008), at a bio-reserve of the Yushan National Park, Taiwan. The climate is characterized by a daily regular cloud immersion and seasonal precipitation (annually above 3,000 mm). Typhoons and accompanying southwest monsoon in summer can cause extremely heavy rainfall. Typhoon Morakot caused landslide here in 2009, and made great changes in both landscape and flora.

Table 1. Changes in community patterns (seedling species diversity, density, and family-level composition) among years 2009, 2010, 2013, and among dynamic models with different percentage of death caused by herbivory (from 65% to 80%).

Community patterns	Field surveys				Dynamic models			
	Year 2009†	Year 2010	Year 2013	*P* ‡ (2009 vs. 2013)	65%	67%	75%	80%
Seedling diversity and density								
Hill N1 index	7.73	9.53	10.42	**	12.3	13.03	14.58	15.95
Seedling density (m^{-2})	0.92	1.19	1.3	NS	1.15	1.1	1	0.9
Family composition ratios §								
Lauraceae	70.65	56.22	55.71	**	24.9	27.18	36.91	35.48
Pentaphylacaceae	8.22	5.96	6.67	NS	1.78	2.12	4.13	6.98
Adoxaceae	6.32	1.55	1.43	**	0.47	0.57	0.69	0.7
Fagaceae	6.10	7.77	8.81	**	3.6	3.76	4.38	4.95
Sapindaceae	0.76	2.59	2.62	**	3.92	3.9	3.9	4.03
Magnoliaceae	0.62	1.30	4.76	**	12.7	13.18	11.28	9.59
Rutaceae	0	12.95	8.10	**	34.22	29.67	17.39	14.57

† Weng *et al*. (2017).

‡ Significance of changes in family-level composition between year 2009 versus 2013 are derived from randomly shuffling years (1,000 times) between the two surveys. * Asterisks indicate statistical significant level. *: $P < 0.05$; **: $P < 0.01$. NS: not significant.

§ Families not shown: Lamiaceae (0.98 → 2.86), Symplocaceae (0.98 → 0), Ericaceae (0.9 → 2.38) were with significant changes in family-level composition from 2009 to 2013; Rosaceae (1.87 → 1.67) and Theaceae (0.84 → 1.19) were not significant.

Vegetation

As censused in 2006, the forest contained 18,766 trees (with diameter at breast height, DBH ≥ 1 cm) belonging to 27 families, 49 genera and 65 species (Yang *et al*., 2008). The most abundant families were Lauraceae, Fagaceae and Theaceae. The forest vegetation was dominated by evergreen broadleaved tree species. The forest type is equivalent to the *Quercus* montane evergreen broadleaved cloud forest defined in Li *et al*. (2013).

The understory communities, first surveyed in 2009 (before Typhoon Morakot), included 60 families, 118 genera and 190 species (Weng *et al*. 2017, in press). The seedling assemblages contained 19 families, 29 genera and 36 tree species with 3,687 individuals, and mostly were found in the families: Lauraceae, Pentaphylacaceae, Adoxaceae, and Fagaceae (Table 1).

Field surveys on tree seedling dynamics and herbivory effects

In order to evaluate the drivers affecting on seedling survival and the consequent species coexistence in seedling bank, we censused the seedling dynamics from February 2010 to January 2013 (monthly before 2012; after 2012, the censusing months are January, April, July, and final census in January, 2013). A total of 324 sites of 1 m^2 sampling unit (Fig. S1) were set to survey compositions of understory plants and tree seedlings (Table S1). Each seedling was tagged uniquely and classified as an old seedling or recruit according to whether it had existed before our first survey. When a recruit was first found, the censusing date would be referred as its "birth date" and its height as "initial height". Then its growth in height, suffered damages, and other surviving states were recorded in each census. When the seedling died, the censusing date was taken as "death date" and its survival duration (number of days) was calculated. The cause of death was categorized into "death by herbivory" and "death by other causes". The former includes deads with feeding signs of herbivore damages and vanishing deads (i.e. newly-germinated seedlings eaten completely by herbivores). The latter included burial, broken-off, drought, nutrient deficiency, and disease-infection, and others (those were hard to clarify if we only found withered or leafless stems).

To assess herbivory effects on seedling survival and growth, the presence of feeding signs on each individual of tree seedling or each species of understory plants in one sampling site was recorded. The sum of presence of feeding signs is taken as the intensity of herbivorous damages across censuses. If the presence of feeding signs on one individual was recorded in consecutive censuses, we only take the first one for a conservative estimate.

To explore whether nurse-plant effects on seedlings by understory plants could reduce herbivory pressure or not, the presence of close neighbors that created shading to one seedling was used to determine the nurse-plant factor, including "with nurse plants" (shaded directly on its top, usually tall herbs or shrubs), "slightly shaded or shaded by others" (such as rock or tree roots), and "no nurse plants or shading".

Fence experiment to examine ungulate herbivory in forest understory

To examine the severity of herbivorous damages on understory plants and tree seedlings from ungulates' foraging, an experiment with fence manipulation was conducted in this plot during August 2011 to February 2012. Five sets of unfenced sites ("unfenced groups" hereafter) and fenced sites ("fenced groups"), each 5 m × 5 m in size and mutually distanced at least 15 m, were bi-monthly censused for counting herbivory-damaged leaves within sites. Fences were 1.2 m in height by using nylon-net enclosures along each side of site, but open at top and mesh which allowed other small mammals, tree-climbing animals or birds to get in. The fenced groups were designed to protect plants only from herbivorous ungulates. We set-up camera traps outside three sites of fenced groups and successfully captured the foraging activities of ungulates outside the fences, confirming that the fences were functional for preventing ungulates.

Almost all native herbivorous or frugivorous mammals had been found in this plot (Hwang and Chian, 2007), such as Formosan Macaque, Formosan Muntjacs, Formosan Sambars, and Formosan Serows. Muntjacs are selective browsers which feed on leaves, shoots, fruits, and etc. Sambars and serows are mixed feeders (browsers and grazers); the former are more often grazers, whereas the latter are more often browsers. These three ungulates are considered the major herbivores in this plot.

Field surveys on environmental factors

To explore environmental effects on seedling survival and growth, we surveyed the cover of moss, litter, root, woody-debris, bare rock, and soil stoniness in each sampling site and measured soil moisture and soil pH (by TDR-100, and IQ-150 meter, respectively, both Spectrum technologies, Inc., USA). Canopy openness was estimated by software "Gap Light Analyzer" (GLA version 2.0) through fisheye hemispherical photography on top of each site (around 1.5 m high). Litter depth was measured at arbitrary three points in each site by using digital vernier caliper.

These environmental factors are treated by principal component analysis (PCA, Fig. S2), and the principal components are abbreviated as "environmental PC"s. Environmental PC1 and PC2 explains 50.7% and 15.7% of variation. Environmental PC1 is positively related to soil pH, soil stoniness, and rock cover, and negatively related to canopy openness, soil moisture, litter depth. Environmental PC2 positively correlates to moss and tree-root cover.

Data analysis

Assessing individual-based seedling survival and growth

To analyze seedling survival and growth, we examine the following variables: (1) individual-based herbivorous damages, the nurse-plant factor and initial height; (2) factors of density-dependent effects for each site, including conspecific and hetero-specific seedling counts and basal areas of adult trees; (3) environmental PC1 and PC2; (4) other neighborhood factors, including tree density, overstory tree basal area, species diversity and mean cover and height of understory plants.

To analyze seedling survival, we used Generalized Linear Mixed Models (GLMM) to examine the individual-based seedling status at the last census (dead = 1, alive = 0) in relation to the aforementioned explanatory variables, using negative binomial distribution with logit link function ("survival model" hereafter). The sampling sites, nested in line transects, were random effects in GLMM, while censusing years were treated as fixed effects to examine inter-annual difference on seedling survival. For the seedling "growth model", we used Gaussian model in GLMM with the identity link function to analyze relative growth rate (RGR) of seedlings (that's, difference between log-transformed height at last censusing date and initial height of living seedlings divided by survival days). GLMM was performed by the R package "glmmADMB".

In order to evaluate herbivory, GLMM was also used to compare leaf damages between unfenced groups and fenced groups in our fence experiments. Leaf damages as the response variable (log-transformed herbivorous-damaged leaves in proportion to total leaves at first census) was analyzed with Gaussian model and the identity link function by using (1) plant height, (2) conspecific and hetero-specific abundance (coverage of understory plants and seedlings in each site), and (3) tree density, overstory tree basal area, species diversity as explanatory variables (Fig. 1).

Dynamic modelling to test species coexistence maintenance in seedling bank

To test our hypothesis that recruitment dynamics mediated by ungulate herbivory is critical to seedling species coexistence, we develop a long-run dynamic model based on controlling the percentage of death by herbivory, as Wright (2002) suggested, that species-specific deaths can dramatically change the conditions of species coexistence. Prior to simulation, we first tested if seedling deaths caused by herbivory were species-specific. To do so, we bootstrapped (1,000 times) the dead seedlings to compute the confidence intervals (CI) for the species-specific percentage of deaths by herbivory (and percentage by other causes, correspondingly) of each species. We found the percentage of death by herbivory are different among species (Fig. 2A). The overall mean observed percentage of death by herbivory compared to deaths by other causes is 67% : 33% in our data.

Then, with different scenarios of percentage of death by herbivory (65%, 67%, 75%, and 80%), we simulate the recruitment dynamics following the steps

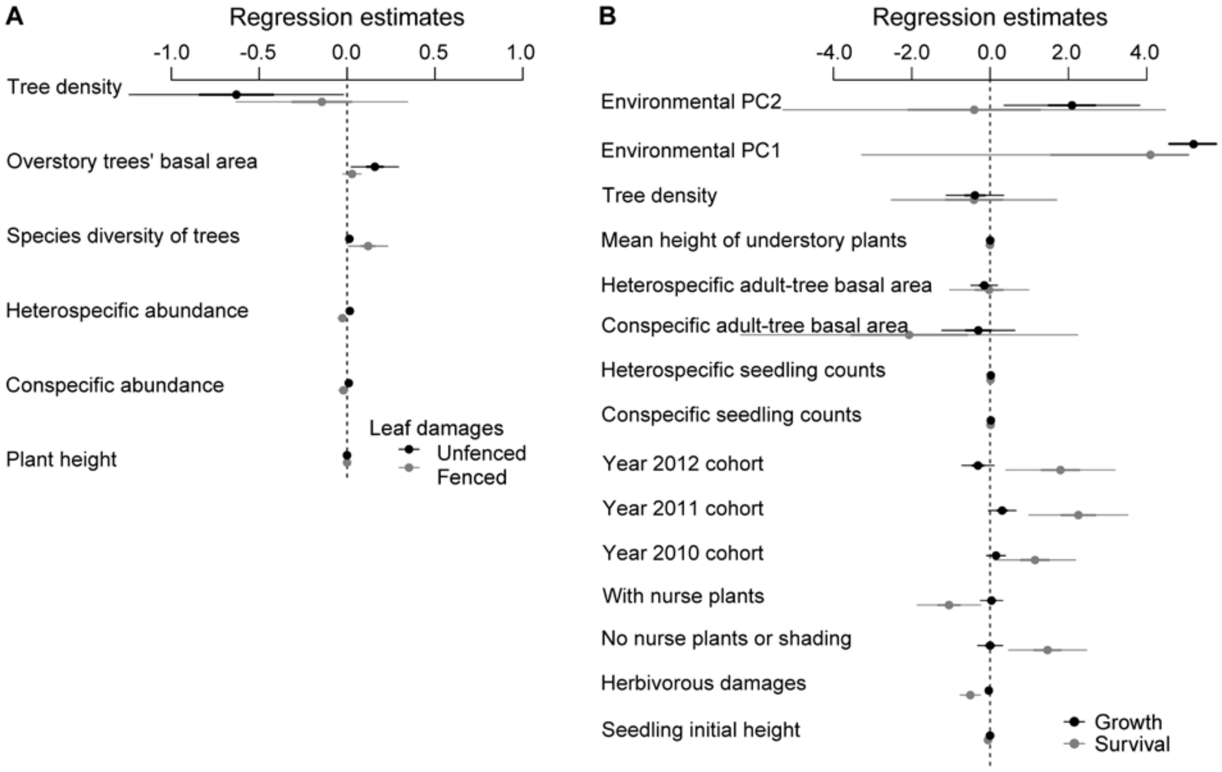

Fig. 1. Significant factors affecting on (**A**) leaf damages of seedlings and understory plants by herbivores in unfenced and fenced (control, in grey) groups; (**B**) 3-yr seedling survival (death event as response, in grey) and growth rate. The estimated fixed effects (in dots) and their 95% confidence interval (CI, in line segments) of each factor were evaluated by a generalized linear mixed-effect model. The CI of factors crossing zero (vertical dash line) indicates no significant effect. The details of estimated values are listed in Table S2 and S3 (Note: dots and line-segments for Environmental PC1 in the growth analysis is out of plot range and not in real scale).

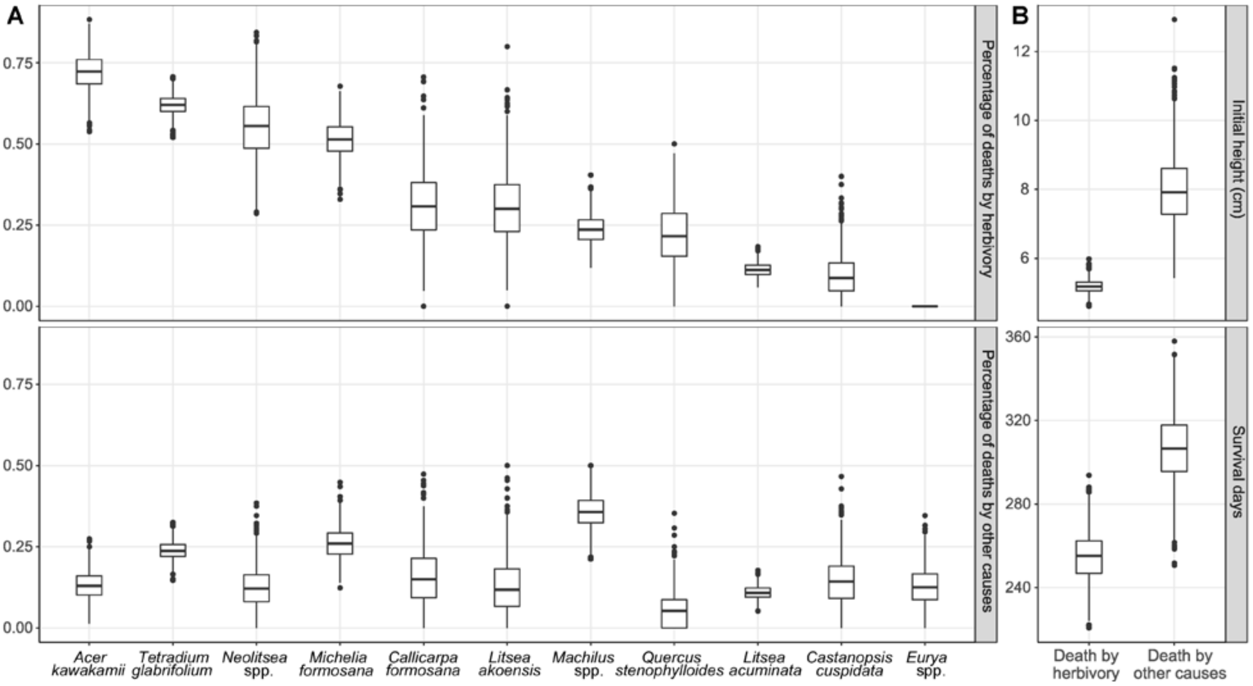

Fig. 2. Comparisons of seedling deaths caused by herbivory relative to other causes (**A**) Percentage of death causes for seedling species and (**B**) distribution of initial height and survival days of the dead seedlings. The confidence intervals (within 0.025–0.975 quantiles) in the boxplot were computed by bootstrapping 1,000 times from the dead seedlings.

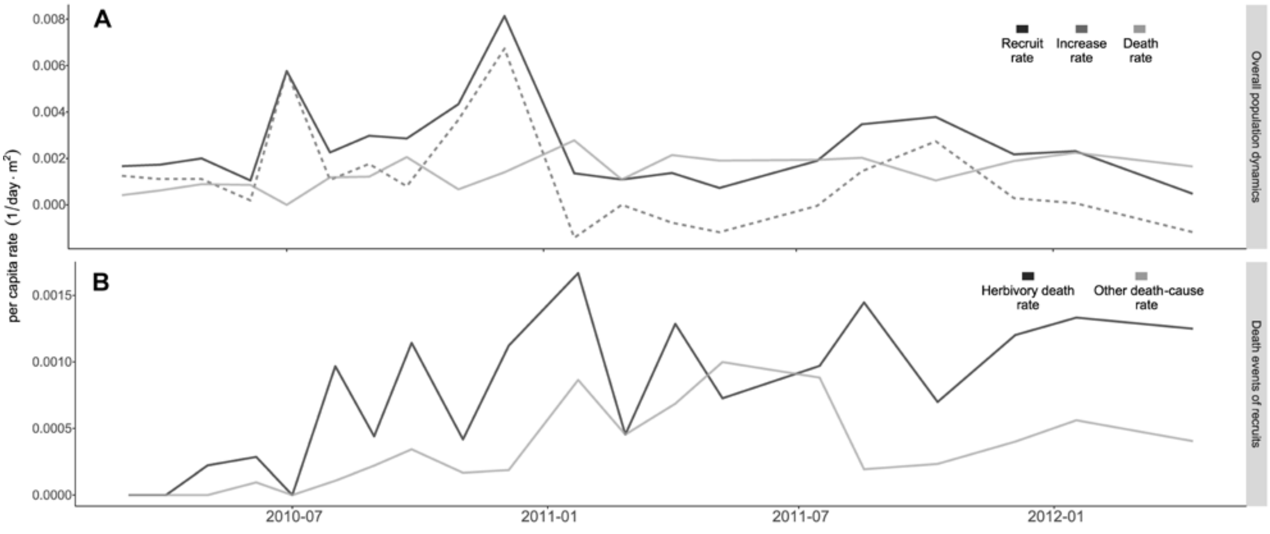

Fig. 3. Observed seedling dynamics during the survey periods: (**A**) Overall recruit rate (dark-grey), death rate (light-grey), and increase rate (computed as recruit rate minus death rate, dash-line); (**B**) Death rate of recruits by herbivory (dark-grey) and other death causes (light-grey). Death rate of recruits by herbivory is positively one-lagged correlated with the overall recruit rate ($R = 0.47$, $P = 0.04$). Local peaks of recruit rate, i.e., bursts of recruitments, occurred at July 2010, November to December 2010, and October 2011.

(see flowchart in Fig. S3): Step 1. Determine the total number of deaths and births (recruitments) at each iteration by bootstrapping 1,000 times from a death and birth distribution, respectively. Here, the death and birth distributions come from estimations for the density function of observed monthly numbers of deaths and recruitments during our survey times (Fig. 3). Step 2. The total number of deaths then can be subdivided into "deaths by herbivory" and "deaths by other causes" in proportion. Step 3. Bootstrap to obtain the species composition for total recruitments, deaths by herbivory, and deaths by other causes from observed species distribution (Fig. 2A, Table S1).

Then in Step 4, to explore how the bio-processes, such as the density-dependent effects, recruitment fluctuations, and apparent competition, can interact with the intense ungulate herbivory in recruitment dynamics, these bio-processes are tested as following (Fig. S3): Step 4.1. Density-dependent deaths for recruitments of each species are removed from seedling bank with a percentage (0–0.5, randomly determined iteratively). The average proportion of density-dependent deaths in modelling (0.25) is consistent with the proportion of observed one-lagged density-dependent deaths immediately after bursts of recruitments during our survey times (Fig. 3). Step 4.2. A small fraction (-1 – +1) for randomly selected species in proportion to their current (log-transformed) abundance are increased or decreased to represent recruitment fluctuations. Another scenario, synchronized recruitments, is also tested. Under synchronized recruitments, we "turn-off" random fluctuations for one species if its recruitments is zero at any iteration; Step 4.3. Deaths due to apparent competition for recruitments among species (sampling K species, with $K \geq 2$, from the current species assemblage), following Usinowicz *et al.* (2012); that is, under apparent competition from species *j*, the effect on deaths for recruits of species *i* can be expressed as:

$$Recruit_i - \frac{Recruit_i}{\left(1+\sum_{j=1}^{K} \propto_{ij} Recruit_j\right)} = \frac{\sum_{j=1}^{K} \propto_{ij} Recruit_j}{\left(1+\sum_{j=1}^{K} \propto_{ij} Recruit_j\right)}$$
(1)

where $\propto_{ij}$ is the competition coefficient, meaning the per capita effect of species *j* on *i*.

Here, we use log-transformed abundance of each seedling species, and fix α_{ij} among the K species for a minimum of log($Recruit_j$) divided by sum of log($Recruit_j$) in modelling. Total deaths for K species due to apparent competition with a random percentage (0.1–0.5) for remaining recruitments (after reduction in 4.1 and 4.2) are assigned to each selected species proportionally according to equation (1). In equation (1), species with lower abundance will suffer more deaths than species with higher abundance from apparent competition; it is the mechanism disfavoring rare species, which may undermine species coexistence.

For each scenario, (percentage of death by herbivory: 65%, 67%, 75%, and 80%), we simulated 200 times (each with 1,000 iterations). Average abundances of seedling species at the final 100 iterations were adopted to compose the final assemblage of seeding bank in each simulation. We compute Hill N1 species diversity index of the final simulated seedling assemblage, which expresses α diversity as "effective number of species" (Hill, 1973; Jost, 2007). Seedling population dynamics along time-lines of 200 times simulation were bootstrapped 1,000 times to compare the increasing or decreasing trend of mean abundance (and 95% CI) among seedling species in the long-run dynamics. All the data analyses and modelling were done in R (R Development Core Team 2016).

DISCUSSION

The seedling assemblages in our 3-yr seedling dynamics censuses contain 20 families, 33 genera and 36 tree species with 953 individuals, including 390 survivals and 563 deads (Table S1). Most seedlings are found in the families: Lauraceae (366), Rutaceae (242), and Magnoliaceae (88); whereas, most survivals are found in families: Lauraceae (226), Fagaceae (34), and Rutaceae (31) (Table S1). Death by herbivory accounts for 377 deads (40% mortality) and other death causes for 186 deads. Ungulate foraging caused most of herbivorous damages in the understory.

Herbivorous ungulates played an important role on seedling survival

Our fence experiment indicates that the major cause of leaf damages in the understory was due to ungulates. The odds ratio for leaf damages caused by herbivores in unfenced groups against fenced groups clearly increased from 0.74 at October, 2011, then 1.17 at December, and finally up to 2.29 at February, 2012. These results indicate that ungulates were responsible for the main cause of leaf damages occurred in unfenced groups.

The herbivorous damages caused by ungulates are significantly related to the following factors through the GLMM analysis (Fig. 1A, and the estimated parameters in Table S3) by comparing the results between fenced groups and unfenced groups. First, herbivorous leaf damages are positively related to the abundance (coverage in each site) of neighboring heterospecific plants (for both understory plants and seedling species); that is, more heterospecific abundance would cause more herbivories, but no such effects due to high conspecific abundance. Therefore, our result does not support negative density dependency from conspecific abundance. Instead, more heterospecific abundance means more understory plants (for their availability on the forest floor are greater than seedlings), which can attract more ungulates' grazing. Second, herbivorous leaf damages are positively related to the effects of overstory basal area. Third, herbivorous leaf damages were negatively related to tree density. From the latter two factors, the attributes of tree formation may attract ungulates' foraging and thereby affect the intensity of herbivory in the understory.

Most of the seedling deaths are caused by ungulate herbivory (40% mortality, Table S1). GLMM analysis on 3-yr seedling survival (Fig. 1B, 563 death events among total 963 individuals) reveals that seedling death can be significantly reduced by nurse-plant effects, i.e., neighboring understory plants as nurse plants for seedlings. Consistently, more deads were found in the seedlings without neighboring nurse plants. In addition, mean height of understory plants in sampling sites had no effects on seedling survival; thus, the understory-plant height cannot help the work out for nurse-plant effects. However, the nearby relationships in space between understory plants and seedling facilitate seedling survival. On the one hand, understory plants provide shelter for shade-tolerant seedlings. On the other hand, at establishment stage, seedling initial height had positive effects on their survival (Fig. 1B). Note that environmental factors in sampling sites had no effects on seedling survival.

Environmental factors do have effects on seedling growth (Fig. 1B, for 390 survivals). The first principal component of environmental factors (environmental PC1) significantly facilitates seedling growth. Analysis of environmental PC1 suggests that less canopy cover or sloping-side (drier and higher soil stoniness, also see Fig. S2) habitats are better for growth due to light availability. Environmental PC1 is negatively related to litter accumulation, which often introduces burials, diseases or pathogens. Specifically, herbivorous damages are still commonly found in the survivals (59.2% damaged, also see Fig. 1B); however, herbivorous damages are not significantly related to seedling growth.

To summarize, micro-environments directly affect on the seedling growth, but not on seedling survival. Seedling survival is greatly threatened by ungulate herbivory. Neighboring understory plants reduce ungulate herbivory pressure for seedlings by nurse-plant effects, thus facilitating seedling survival.

Herbivory causes species-specific death, generally on the very early stage of recruits

In our plot, even though ungulates are not species-specific herbivores, the percentage of death by herbivory are species-specific, and not evenly distributed, among abundant seedling species (Fig. 2A). Such differences were likely due to the differential resistance (e.g., shade-tolerance, initial height) among seedling species. For example, the two seedling species with highest percentage of death by herbivory, *Acer kawakamii* and *Tetradium glabrifolium*, are light-demanding. Seedlings that are easily found by browsers are usually light-demanding seedlings in open habitats, growing without shading nearby. Compared with seedlings died of other death causes, seedlings which died of herbivory are characterized by lower

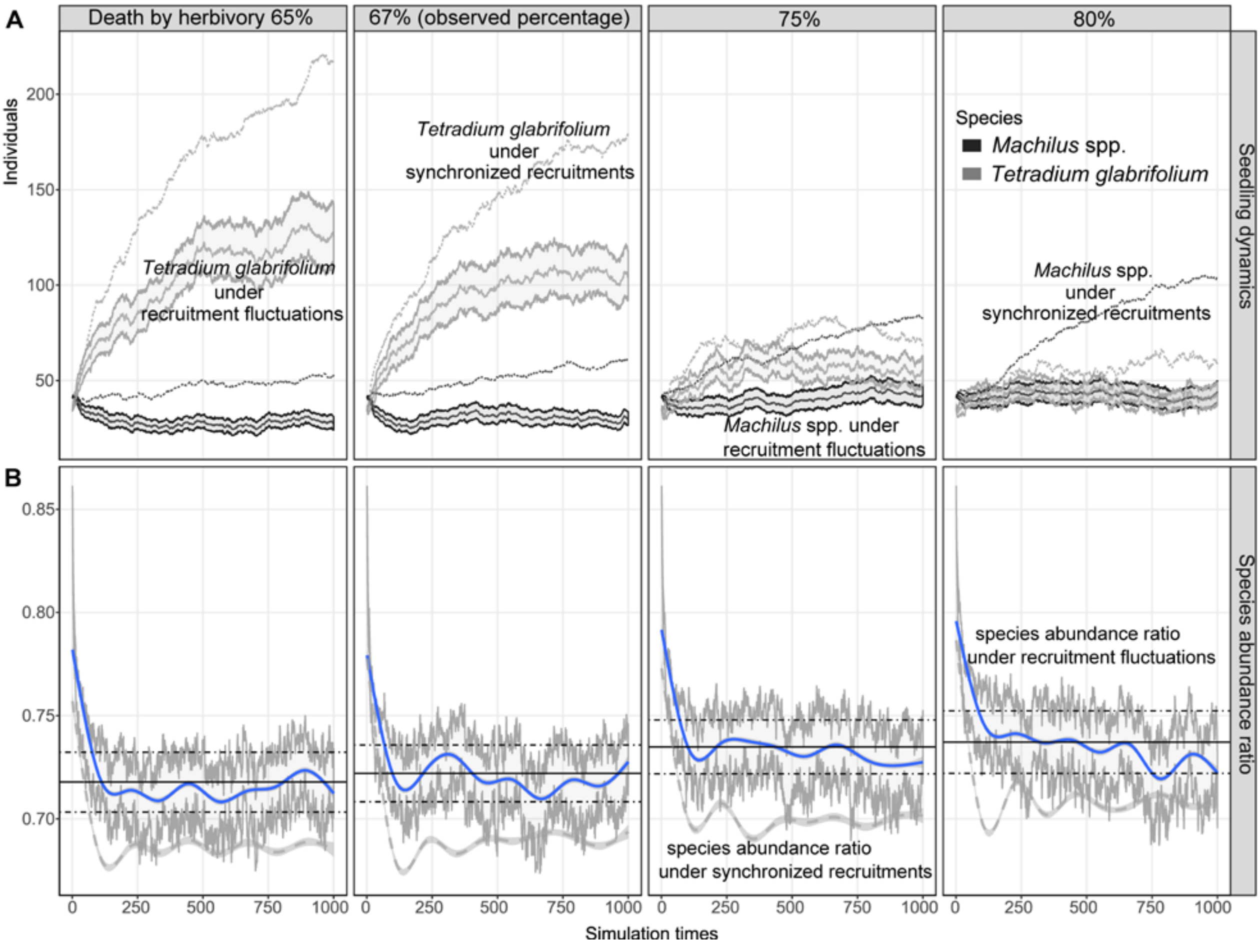

Fig. 4. A dynamic model simulating seedling assemblage dynamics of (**A**) abundant species populations and (**B**) changes of species abundances compared to the initial value (named species abundance ratio). Increasing percentage of death by herbivory, from 65%, 67% (observed percentage in the field), 75%, to 80%, can clearly change the community dynamics: suppressing *Tetradium glabrifolium* (in light-grey) but promoting *Machilus* spp. (in dark-grey). The confidence interval (within 0.025–0.975 quantiles, grey-shaded region) were computed by bootstrapping 1,000 times from 200 simulations with 1,000 iterations in each scenario. With increased the percentage of death by herbivory, total means of species abundance ratio (horizontal solid line in lower part, with ±sd in the dotted-dash lines) also slightly uplift. Under synchronized recruitments, i.e., without recruitment fluctuations for each species, abundant species, such as *T. glabrifolium* or *Machilus* spp., become substantially more dominant (only mean values are shown as dash lines in upper panels). Species abundance ratio (in dash lines) under synchronized recruitments is significantly lower than that under recruitment fluctuations. Flowchart of this dynamic model is in Fig. S3. Simulations results of other species are shown in Fig. S4.

initial height and shorter survival days (Fig. 2B). Therefore, most predated seedlings were just in their very early days since germinated. Newly-germinated seedlings are preferred by ungulate. Their lower initial height resulted in the higher susceptibility to death after being damaged, and thereby large number of seedling deaths were “vanishing” (53.5% of the death by herbivory) (i.e. the whole plants were eaten).

In contrast, the percentage of death by other causes are not so different among species, but are consistently low, except for *Machilus* spp. Among other death causes (Fig. 2A), some of them may be induced by species-specific diseases or infections, which were not easily discerned in our censuses. There are still some of other death causes, such as burial, broken-off, drought, and nutrient deficiency that may be affected by some species-specific traits. But in our results, the percentages of death caused by other factors are generally lower (33%) than the species-specific deaths caused by herbivory (67%), and are more likely non-discriminatory among species.

The temporal dynamics of seedling populations shows aperiodic variations in the 3-yr duration (2010–2013, Fig. 3). The local peak of recruit rate, which represents the occurrence of bursts of recruitments, occurred at July 2010, November to December 2010, and October 2011. A total of 24 species (Table S1) had joined the synchronous recruitment events. The bursts of recruitments were followed (one-lagged) by greater herbivory mortality, accounting for 24.4%, 22.4% and 31.8%, respectively. Seedling death caused by herbivory along time-lines was correlated with the overall recruit rate at one-lag (R = 0.47, P = 0.04). In contrast, seedling death by other causes exhibited no such correlations with the lagged recruit rate (Fig. 3B). These findings suggest that the intensity of density-dependent effects resulted in one-fourth to one-third of recruits eaten by herbivores immediately after the bursts of recruitments. The negative density dependency occurred at the community level in time span, but was not significant at species level (see conspecific seedling or adult-tree species effects, Fig. 1B) according to our analyses on survival. We found no significant negative density dependency induced from conspecific abundance. This is most likely because the main herbivores, ungulates, are not specialists to seedling species. The results that density-dependent deaths at the community level can attract more herbivores after the bursts of recruitments (Fig. 3B) also suggests apparent competition may occur and may decrease the abundance of seedling species which are less resistant to ungulate herbivory, such as those with lower initial height (Fig. 2A, B).

Modelling results showing raising percentage of deaths by herbivory mediates recruitment dynamics

Our dynamic model helps us to explore how species coexistence can still be maintained under intense ungulate herbivory. We suggest the following scenarios:

Raising percentage of death by herbivory

Differences in species-specific deaths by herbivory result in changes of recruitment dynamics. As we have already known, light-demanding species suffer higher percentage of deaths by herbivory than shade-tolerant ones. The dominance of *T. glabrifolium* (a light-demanding species), for example, greatly overwhelms the abundant shade-tolerance species (in the field) such as Lauraceae species if we maintain or slightly lower the percentage of death by herbivory (65%, correspondingly increasing the percentage of death by other causes to 35%) (Fig. 4A; or Table 1, see Rutaceae for family-level composition).

We simulated not only differences in species-specific deaths, but also by randomly shuffling total numbers of births and deaths iteratively during simulations. However, lower percentage of death by herbivory (65%–67%), and correspondingly greater chance deaths (from other death causes), simply cannot prevent abundant species from becoming more dominant after bursts of recruitments (Fig. 4A). In contrast, by raising percentage of deaths by herbivory to 75% and 80%, the abundance of *T. glabrifolium* is greatly reduced (Fig. 4A). In addition, we also find a decline in *Michelia formosana* (another light-demanding species, in Fig. S4A, or see Magnoliaceae in Table 1), but steady rise in *Machilus* spp. (shade-tolerant species in Lauraceae, Fig. 4A) or maintain the abundance in *Litsea acuminata* (Fig. S4A, Lauraceae in Table 1). While, other rare seedling species still can maintain their small populations with occasional bursts of recruitment, such as *A. kawakamii* (Sapindaceae in Table 1) and *Neolitsea* spp.

In the model results, species richness can be recovered from bursts of deaths, even when increasing deaths by herbivory, and seedling assemblages can be re-constructed under different scenarios (Fig. 4B). Comparing to the real situation in the field: after Typhoon Morakot, more open habitats were created in this plot in 2009, which lead to colonization of more light-demanding families (increase in Rutaceae, Magnoliaceae, Sapindaceae), and the seedling diversity had increased from 2010 to 2013 (Table 1). In our modelling, with increasing percentage of deaths by herbivory (65%–80%), seedling species diversity increases, and the family-level compositions are more similar as our final census on 2013 (Table 1), with higher proportions of shade-tolerant families (Lauraceae, Pentaphylacaeae, Fagaceae) and fewer light-demanding families (Rutaceae, Magnoliaceae, Sapindaceae). It suggested that the community assembly gradually recovered and implied that ungulate herbivory likely had affected on this long-term regeneration process.

Recruitment fluctuations and apparent competition

We find that rare species really benefited from (random) recruitment fluctuations under the phenomenon of bursts of recruitments. Bursts of recruitments also mean that large proportions of recruitments are synchronized (as it indeed occurred in the field (Fig. 3)). If we removed (random) recruitment fluctuations in the dynamic model, synchronized recruitments facilitate the dominance of abundant species, such as *T. glabrifolium* and *Machilus* spp. (Fig. 4A). Synchronized recruitments increase the chance of apparent competition on rare species, and undermines their fragile populations. Effect of synchronized recruitments on seedling assemblage thus has two sides: facilitating recruitment (seedling density enhanced to 1.39 – 1.9, compared to 0.9 – 1.15 with recruitment fluctuations, Table 1), while decreasing species diversity from 15.95 (Table 1) down to 9.27. In other words, rare seedling species benefited under fluctuating recruitments but were disfavored by synchronized recruitments.

The dynamic model demonstrates how recruit dynamics interact with ungulate herbivory

Through raising percentage of death caused by herbivory, in combination of density-dependent mortality and recruitment fluctuations, seedling species diversity and species richness can be enhanced in the model (Table 1, see Hill N1 diversity; species richness in Fig. 4B). Speculative but interesting, it is somewhat consistent with the changing seedling assemblages since Typhoon Morakot, 2009. Our dynamic model provides further insights into how recruitment dynamics can interact with ungulate herbivory, co-operating with some long-term processes which were hard to evaluated or observed, such as chance bursts of recruitments or death events, recruitment fluctuations, or apparent competition.

In conclusion, intense ungulate herbivory exerted significant effects on species-specific mortality of seedlings. However, ungulate herbivory is not really detrimental to maintenance of seedling species coexistence; rather, ungulate herbivory changes the recruitment dynamics, as found both in the field and in modelling.

ACKNOWLEDGEMENTS

We thank Bo-kai Ciou for help in surveying herbivory for the fence experiment and preparing raw-data, as well as animal species captured from camera traps. Dr. Kuoh-Cheng Yang and Jer-ker Lin provided the tree data in Nanhsi FDP. We also thank Dr. Chung-Yi Lin for providing valuable information on ungulate foraging behaviors. This study was supported by Yushan National Park and Taiwan Forestry Bureau.

LITERATURE CITED

Asquith, N.M., **S.J. Wright** and **M.J. Clauss**. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology **78(3)**: 941-946.

Bachelot, B., **M. Uríarte**, **J. Thompson** and **J.K. Zimmerman**. 2016. The advantage of the extremes: tree seedlings at intermediate abundance in a tropical forest have the highest richness of above-ground enemies and suffer the most damage. J. Ecol. **104(1)**: 90-103.

Bagchi, R., **R.E. Gallery**, **S. Gripenberg**, **S.J. Gurr**, **L. Narayan**, **C.E. Addis**, **R.P. Freckleton**, and **O.T. Lewis**. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature **506(7486)**: 85-88.

Baraloto, C., and **P.-M. Forget**. 2007. Seed size, seedling morphology, and response to deep shade and damage in neotropical rain forest trees. Am. J. Bot. **94(6)**: 901-911.

Comita, L.S., **S.A. Queenborough**, **S.J. Murphy**, **J.L. Eck**, **K. Xu**, **M. Krishnadas**, **N. Beckman**, and **Y. Zhu**. 2014. Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J. Ecol. **102(4)**: 845-856.

Curran, L.M., and **C.O. Webb**. 2011. Experimental Tests of the Spatiotemporal Scale of Seed Predation in Mast-Fruiting Dipterocarpaceae. Ecol. Monogr. **70(1)**: 129-148.

Dearing, M.D., **A.M. Mangione**, and **W.H. Karasov**. 2000. Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. Oecologia **123(3)**: 397-405.

Dyer, L.A., **D.K. Letourneau**, **G.V. Chavarria**, and **D.S. Amoretti**. 2010. Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. Ecology **91(12)**: 3707-3718.

George, L.O., and **F.A. Bazzaz**. 1999. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology **80(3)**: 846-856.

Green, P.T., **K.E. Harms**, and **J.H. Connell**. 2014. Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. PNAS **111(52)**: 18649-18654.

Harms, K.E., **S.J. Wright**, **O. Calderón**, **A. Hernández**, and **E.A. Herre**. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404(6777)**: 493-495.

Hidding, B., **J.P. Tremblay**, and **S.D. Côté**. 2012. Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities. For. Ecol. Manage. **276**: 96-103.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology **54(2)**: 427-432.

Holt, R. D. 1977. Predation, Apparent Competition, and the Sctructure of Prey Communities. Theor. Popul. Biol. **12(2)**: 197-229.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science **203(4387)**: 1299-1309.

Hulme, P.E. 1996. Herbivory, plant regeneration, and species coexistence. J. Ecol. **84(4)**: 609-615.

Hwang, M.H., and **Y.Y. Chian**. 2007. Monitoring larger mammals in the Nanzihshian logging road area, Yushan National Park, Taiwan. Taiwan J. For. Sci. **22**: 135-148.

Jansen, P. a, **F. Bongers** and **L. Hemerik**. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecol. Monogr. **74(4)**: 569-589.

Jost, L. 2007. Partitioning diversity into independnet alpha andf beta components. Ecology **88(10)**: 2427-2439.

Kobe, R.K., and **C.F. Vriesendorp**. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecol. Lett. **14(5)**: 503-510.

Li, C.-F., **M. Chytrý**, **D. Zelený**, **M.-Y. Chen**, **T.-Y. Chen**, **C.-R. Chiou**, **Y.-J. Hsia**, **H.-Y. Liu**, **S.-Z. Yang**, **C.-L. Yeh**, **J.-C. Wang**, **C.-F. Yu**, **Y.-J. Lai**, **W.-C. Chao**, and **C.F. Hsieh**. 2013. Classification of Taiwan forest vegetation. Appl. Veg. Sci. **16(4)**: 698-719.

Lischke, H., and **T.J. Löffler**. 2006. Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. Ecol. Modell. **198(3-4)**: 341-361.

Norghauer, J.M., and **D.M. Newbery**. 2014. Herbivores differentially limit the seedling growth and sapling recruitment of two dominant rain forest trees. Oecologia **174(2)**: 459-469.

Paine, C.E.T., **H. Beck**, and **J. Terborgh**. 2016. How mammalian predation contributes to tropical tree community structure. Ecology **97(12)**: 3326-3336.

Royo, A.A., and **W.P. Carson**. 2005. The herb community of a tropical forest in central Panamá: dynamics and impact of mammalian herbivores. Oecologia **145(1)**: 66-75.

Royo, A.A., and **W.P. Carson**. 2008. Direct and indirect effects of a dense understory on tree seedling recruitment in temperate forests: habitat-mediated predation versus competition. Can. J. For. Res. **38(6)**: 1634-1645.

Royo, A.A., **R. Collins**, **M.B. Adams**, **C. Kirschbaum**, and **W.P. Carson**. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology **91(1)**: 93-105.

Smit, C., and **C. Vandenberghe**. 2007. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. Oecologia **152(2)**: 265-273.

Usinowicz, J., **S.J. Wright**, **A.R. Ives**, and **D.F. Doak**. 2012. Coexistence in tropical forests through asynchronous variation in annual seed production. Ecology **93(9)**: 2073-2084.

Weng, C.-Y., **K.-C. Yang**, **C.-F. Hsieh**, **C.-H Hsieh**, and **M.-H. Su**. 2017. Local neighborhood communities in the understory play a critical role by affecting regeneration niches and subsequent community assembly in a montane cloud forest. Ecological Research: (Online First)

Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia **130(1)**: 1-14.

Wright, S.J., **H.C. Muller-Landau**, **O. Calderón**, and **A. Hernandéz**. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology **86(4)**: 848-860.

Yang, K.-C., **J.-K. Lin**, **C.-F. Hsieh**, **C.-L. Huang**, **Y.-M. Chang**, **L.-H. Kuan**, **J.-F. Su**, and **S.-T. Chiu**. 2008. Vegetation pattern and woody species composition of a broad-leaved forest at the upstream basin of Nantzuhsienhsi in mid-southern Taiwan. Taiwania **53(4)**: 325-337.

Taiwania 62(3): S1–S6, 2017

DOI: 10.6165/tai.2017.62.283

Supplementary data

Weng *et al.* 2017. Recruitment dynamics mediated by ungulate herbivory can affect species coexistence for tree seedling assemblages. **Taiwania** 62(3): 283-293. (DOI: 10.6165/tai.2017.62.283)

Table S1. Species composition of tree seedlings, and the numbers of recruitments, survivals, deaths, deaths by herbivory, deaths by other causes, average of relative growth rate and frequency of occurrence in the Nanhsi forest dynamics plot, Taiwan.

Family and species		Recruit		Total	Survival	Death	Mortality	Death by herbivory		Death by other causes		Relative growth rate‡	Frequency
		Total	† In bursts										
Lauraceae	*Litsea acuminata*	61	29	216	167	49	22.7%	25	(51%)	24	(49.0%)	0.00017	125
	Machilus spp.	64	35	100	40	60	60.0%	24	(40%)	36	(60.0%)	0.00025	81
	Neolitsea spp.	22	8	30	9	21	70.0%	17	(81%)	4	(19.0%)	0.00012	28
	Litsea akoensis	8	5	15	8	7	46.7%	5	(71.4%)	2	(28.6%)	0.00042	14
	Cinnamomum insularimontanum	3	1	5	2	3	60.0%	2	(66.7%)	1	(33.3%)	0.00011	5
Rutaceae	*Tetradium glabrifolium*	225	90	240	31	209	87.1%	151	(72.2%)	58	(27.8%)	0.00091	53
	Zanthoxylum ailanthoides	2	1	2	0	2	100.0%	2	(100%)	0	(0.0%)		2
Magnoliaceae	*Michelia formosana*	87	35	88	19	69	78.4%	46	(66.7%)	23	(33.3%)	0.00066	60
Sapindaceae	*Acer kawakamii*	61	12	63	4	59	93.7%	50	(84.7%)	9	(15.3%)	0.00000	32
	Acer albopurpurascens	1	0	1	1	0	0.0%	0	(0%)	0	(0.0%)	0.00000	1
Fagaceae	*Castanopsis cuspidata*	7	1	21	16	5	23.8%	2	(40%)	3	(60.0%)	0.00029	20
	Quercus stenophylloides	9	1	16	11	5	31.2%	4	(80%)	1	(20.0%)	0.00016	15
	Lithocarpus kawakamii	1	0	8	7	1	12.5%	1	(100%)	0	(0.0%)	0.00027	8
Pentaphylacaceae	*Eurya* spp.	9	0	30	26	4	13.3%	0	(0%)	4	(100.0%)	0.00038	26
Lamiaceae	*Callicarpa formosana*	16	4	18	9	9	50.0%	6	(66.7%)	3	(33.3%)	0.00105	17
	Clerodendrum trichotomum	8	2	10	2	8	80.0%	4	(50%)	4	(50.0%)	0.00000	8
Rosaceae	*Pourthiaea beauverdiana*	8	1	12	7	5	41.7%	3	(60%)	2	(40.0%)	0.00055	12
	Malus doumeri	3	0	3	0	3	100.0%	3	(100%)	0	(0.0%)		1
	Eriobotrya deflexa	0	0	1	0	1	100.0%	1	(100%)	0	(0.0%)		1
Elaeocarpaceae	*Elaeocarpus sylvestris*	14	9	14	2	12	85.7%	6	(50%)	6	(50.0%)	0.00000	12
Araliaceae	*Aralia bipinnata*	11	2	13	2	11	84.6%	8	(72.7%)	3	(27.3%)	0.00141	11
Ericaceae	*Rhododendron leptosanthum*	1	0	10	8	2	20.0%	2	(100%)	0	(0.0%)	0.00032	8
	Vaccinium randaiense	0	0	2	2	0	0.0%	0	(0%)	0	(0.0%)	0.00001	2
Salicaceae	*Salix fulvopubescens*	5	3	5	1	4	80.0%	4	(100%)	0	(0.0%)	0.00071	4
	Xylosma congesta	3	1	4	3	1	25.0%	1	(100%)	0	(0.0%)	0.00032	3
Theaceae	*Schima superba*	6	4	6	1	5	83.3%	5	(100%)	0	(0.0%)	0.00069	6
	Gordonia axillaris	1	1	1	1	0	0.0%	0	(0%)	0	(0.0%)	0.00060	1
Adoxaceae	*Viburnum taitoense*	0	0	6	5	1	16.7%	0	(0%)	1	(100%)	0.00018	5
	Viburnum luzonicum	0	0	1	0	1	100.0%	1	(100%)	0	(0.0%)		1
Betulaceae	*Alnus formosana*	3	1	3	2	1	33.3%	1	(100%)	0	(0.0%)	0.00050	3
Urticaceae	*Oreocnide pedunculata*	2	1	3	1	2	66.7%	1	(50.0%)	1	(50.0%)	0.00104	3
Oleaceae	*Fraxinus griffithii*	1	0	1	1	0	0.0%	0	(0.0%)	0	(0.0%)	0.00158	1
	Osmanthus matsumuranus	1	1	1	1	0	0.0%	0	(0.0%)	0	(0.0%)	0.00016	1
Pittosporaceae	*Pittosporum illicioides*	2	0	2	0	2	100.0%	1	(50.0%)	1	(50.0%)		2
Symplocaceae	*Symplocos* spp.	1	1	1	0	1	100.0%	1	(100.0%)	0	(0.0%)		1
Taxaceae	*Cephalotaxus wilsoniana*	0	0	1	1	0	0.0%	0	(0.0%)	0	(0.0%)	0.00000	1
	Total summary	646	249	953	390	563	59.1%	377	(67.0%)	186	(33.0%)	0.00036	258

† Recruits censused in bursts of recruitments, occurring at July 2010, November to December 2010, and October 2011.

‡ Only taking averages of positive relative growth rates among seedling survivals.

Table S2. Results of mixed-effect models for seedling survival and growth.

Variable	Survival†			Growth‡		
	Estimate	Standard error	*P*	Estimate	Standard error	*P*
(Intercept)	0.038	0.77	0.96	-0.035	0.22	0.88
Environmental PC2	-0.405	2.49	0.87	2.091	0.88	0.02*
Environmental PC1	4.093	3.76	0.28	7.937	1.39	< 0.01**
Tree density	-0.409	1.08	0.70	-0.386	0.37	0.30
Mean height of understory plants	-0.003	0.00	0.47	0.003	0.00	0.04*
Heterospecific adult-tree basal area	-0.025	0.51	0.96	-0.15	0.17	0.39
Conspecific adult-tree basal area	-2.067	2.20	0.35	-0.301	0.48	0.53
Heterospecific seedling counts	0.012	0.02	0.50	0.018	0.01	< 0.01**
Conspecific seedling counts	0.011	0.02	0.53	0.019	0.01	< 0.01**
Year 2012 cohort	1.797	0.71	0.01*	-0.31	0.21	0.14
Year 2011 cohort	2.252	0.64	< 0.01**	0.308	0.18	0.09
Year 2010 cohort	1.147	0.53	0.03*	0.15	0.12	0.22
With nurse-plants	-1.049	0.41	0.01*	0.037	0.14	0.80
No nurse-plants or shading	1.467	0.51	< 0.01**	0	0.16	1.00
Herbivorous damages	-0.504	0.13	< 0.01**	-0.033	0.03	0.33
Seedling initial height	-0.053	0.01	< 0.01**	-0.002	0.00	0.17

† Survival: GLMM with negative binomial distribution and logit link (*N* = 953, with 563 deaths, 390 survivals).

‡ Growth: GLMM with Gaussian distribution and identity link (*N* = 390).

* Asterisks indicate statistical significant level. *: *P* < 0.05; **: *P* < 0.01. NS: not significant.

Table S3. Results of mixed-effect models for herbivorous leaf damages in the fence experiment.

Variable	Unfenced groups†			Fenced groups		
	Estimate	Standard error	*P*	Estimate	Standard error	*P*
(Intercept)	-0.2140	0.1100	0.04*	-0.1090	0.0900	0.25
Tree density	-0.6300	0.3100	0.04*	-0.1430	0.2500	0.56
Ovestory trees' basal area	0.1580	0.0700	0.02*	0.0280	0.0300	0.28
Species diveristy of trees	0.0130	0.0100	0.23	0.1200	0.0600	0.04*
Heterospecific abundance	0.0160	0.0100	< 0.01**	-0.0260	0.0100	0.04*
Conspecific abundance	0.0100	0.0100	0.14	-0.0210	0.0100	0.13
Plant height	-0.0004	0.0002	0.12	-0.0001	0.0002	0.60

† GLMM with Gaussian distribution and identity link (*N* = 134 for unfenced groups, and *N* = 136 for fenced groups).

* Asterisks indicate statistical significant level. *: *P* < 0.05; **: *P* < 0.01. NS: not significant.

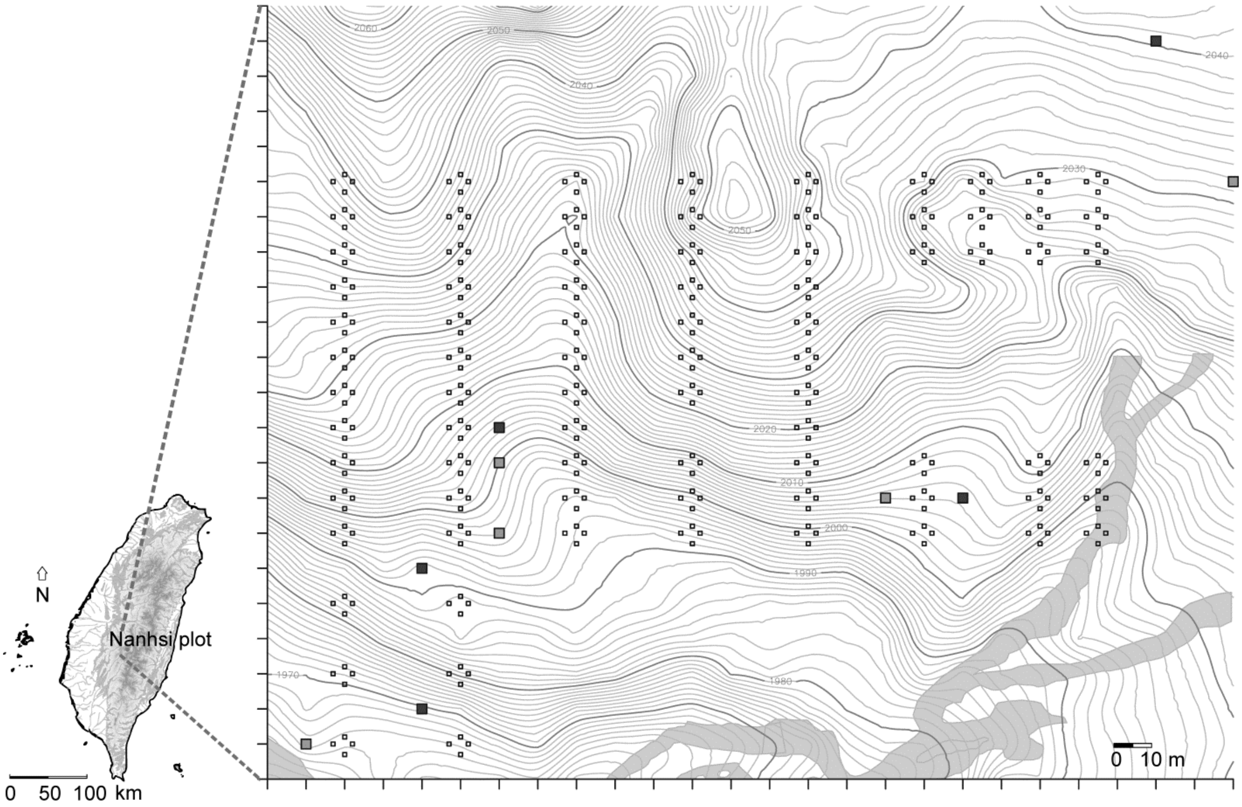

Fig. S1. Field survey of this study in Nanhsi forest dynamics plot. The open squares indicate the 324 sites of 1 m × 1 m sampling unit for surveying seedling dynamics (2010–2013). Grey grid squares indicate the five sets of unfenced sites (“unfenced groups” in light-grey) and fenced sites (“fenced groups” in dark-grey), each 5 m × 5 m in size and mutually distanced at least 15 m. The fence manipulation was used to study the effects of ungulate herbivory on leaf damages in forest understory (August 2011 to February 2012). Valley region are shaded in this contour map.

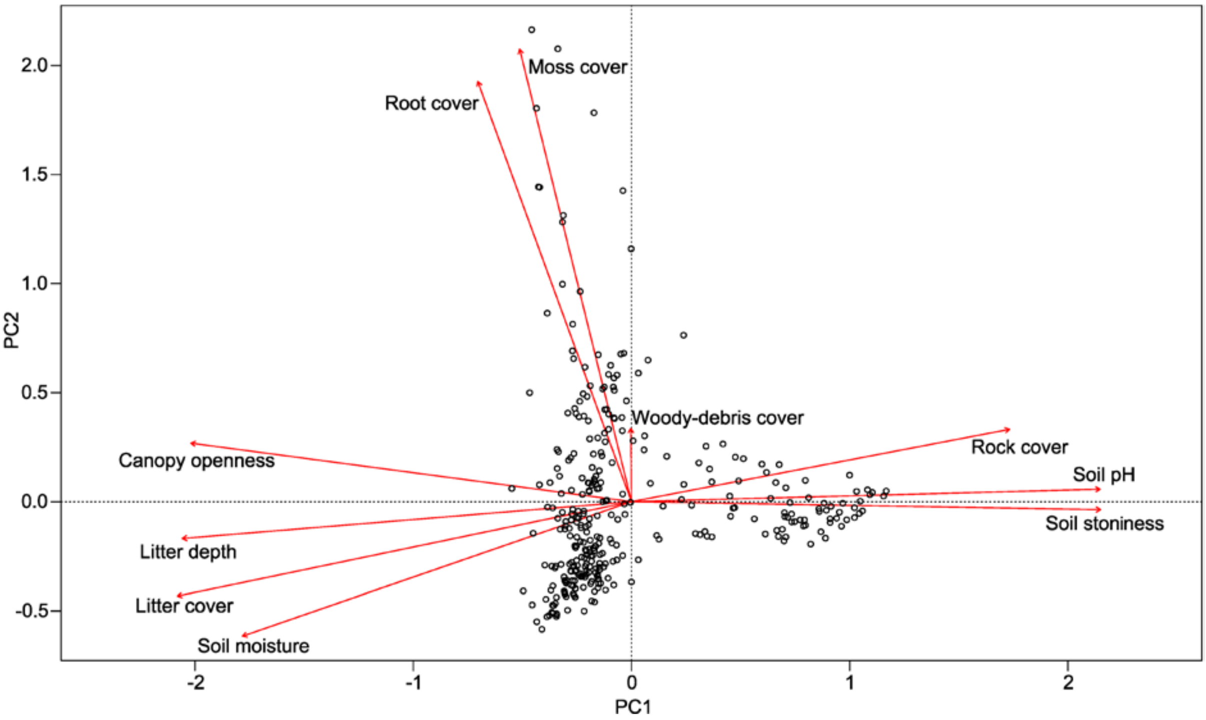

Fig. S2. Biplot of the principal component analysis (PCA) for the environmental factors. Variance explained by the biplot is 66.4% (PC1: 50.7%; PC2: 15.7%). The open circles represent site scores (*N* = 324) which ordinate on the biplot. Red marks with arrows highlight the environmental factors most associated with the principal components. PC1 is positively related to soil pH, soil stoniness, and rock cover, and negatively related to canopy openness, soil moisture, litter depth, and litter cover. PC2 positively correlates to moss, tree root , and woody-debris cover.

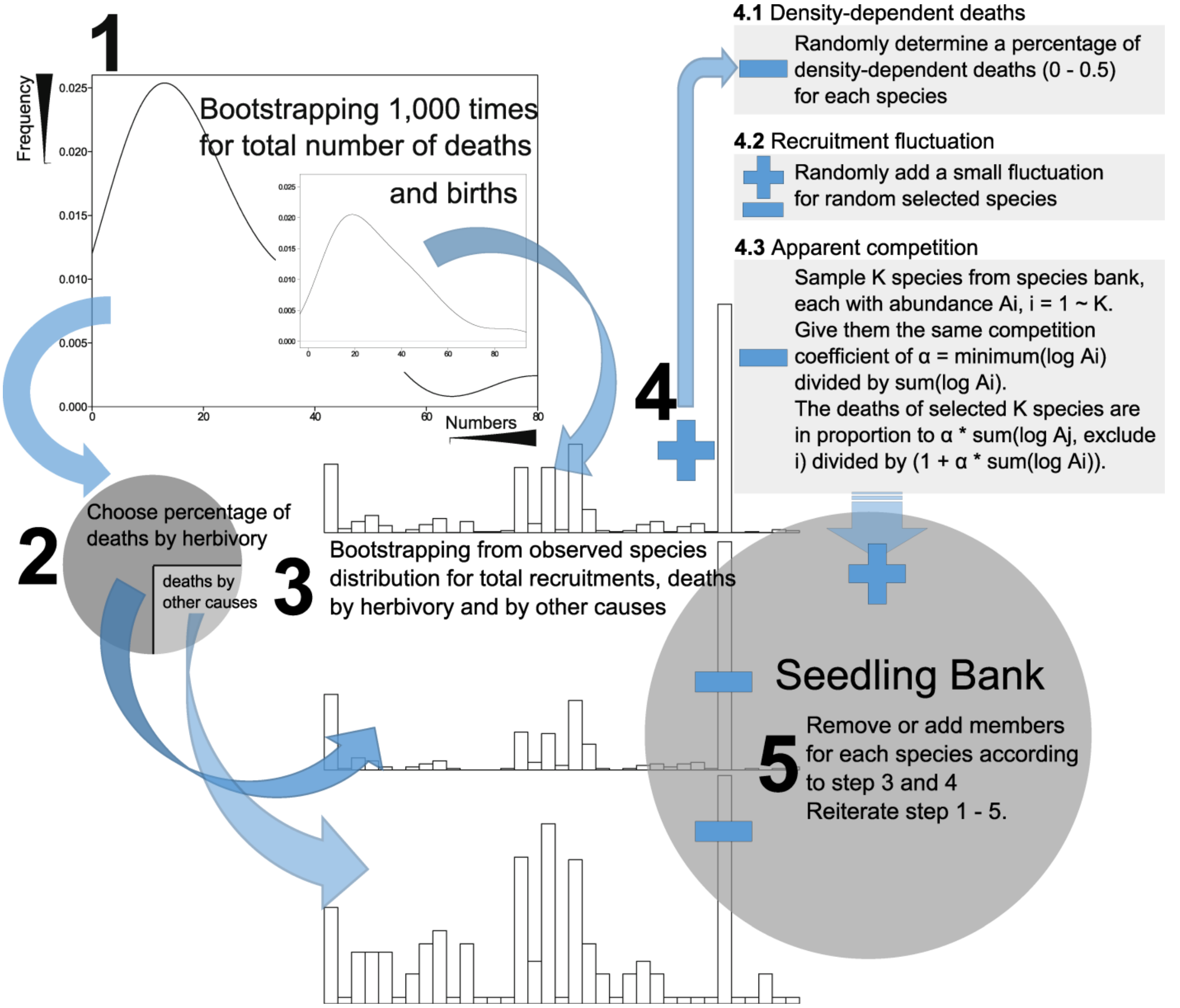

Fig. S3. Flowchart explaining the dynamic model simulating seeding assemblage dynamics by controlling the percentage of death by herbivory. Each simulation runs 1,000 iterations and each iteration includes step 1–5. (1) Determine total number of deaths and births (recruitments) by bootstrapping from the death and birth distribution, respectively. The death and birth distribution is the kernel density estimation according to the monthly number of deaths and recruitments from empirical data during our survey periods. (2) Subdivide total number of deaths into deaths by herbivory and by other causes. (3) Compute species-specific recruitments and deaths by bootstrapping from observed species distribution for recruitments, deaths by herbivory and by other causes (Fig 2, Table S1). (4) Recruitments for each species are reduced ("-" symbol) by a random percentage (0–0.5, iteratively) as a result of density-dependent deaths (following 4.1 in the figure); increased ("+" symbol) or decreased ("-" symbol) due to random fluctuation (following 4.2 in the figure); reduced by deaths due to apparent competition, which is determined by a random percentage (0.1–0.5) of the remaining recruitments (after reduction in 4.1, 4.2) and assigned to species according to the abundance distribution (following 4.3 in the figure). (5) Remove or add members in current seedling bank. Then, reiterate step 1–5. We perform 200 simulations for each percentage of death by herbivory (65%, 67%, 75%, and 80%).

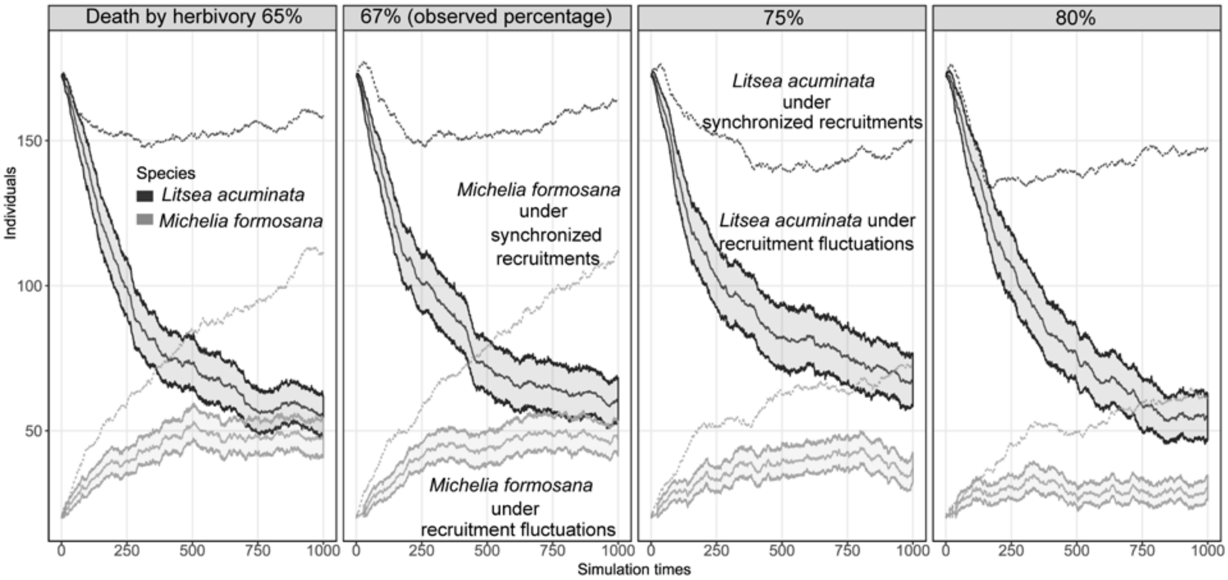

Fig. S4. Species dynamics simulated by the dynamic model for examining coexistence of tree seedling species under different percentages of death by herbivory. Increasing percentage of death by herbivory, from 65%, 67% (observed percentage in the field), 75%, to 80%, can suppress *Michelia formosana* (in light-grey) but not affect *Litsea acuminata* (in dark-grey). The confidence interval (within 0.025–0.975 quantiles, grey-shaded region) were computed by bootstrapping 1,000 times from 200 simulations with 1,000 iterations in each scenario. Under synchronized recruitments, i.e., without (random) recruitment fluctuations, both *L. acuminata* and *M. formosana* become substantially more abundant (only mean values are shown as dash lines in upper panel).