



Title	The contribution of seed dispersers to tree species diversity in tropical rainforests
Author(s)	Kakishima, Satoshi; Morita, Satoru; Yoshida, Katsuhiko; Ishida, Atsushi; Hayashi, Saki; Asami, Takahiro; Ito, Hiromu; Miller, Donald G.; Uehara, Takashi; Mori, Shigeta; Hasegawa, Eisuke; Matsuura, Kenji; Kasuya, Eiiti; Yoshimura, Jin
Citation	Royal Society open science, 2(10), 150330 https://doi.org/10.1098/rsos.150330
Issue Date	2015-10-14
Doc URL	http://hdl.handle.net/2115/66437
Rights(URL)	https://creativecommons.org/licenses/by/4.0/
Type	article
File Information	150330.full.pdf



[Instructions for use](#)



Cite this article: Kakishima S *et al.* 2015 The contribution of seed dispersers to tree species diversity in tropical rainforests. *R. Soc. open sci.* 2: 150330.
<http://dx.doi.org/10.1098/rsos.150330>

Received: 9 July 2015

Accepted: 17 September 2015

Subject Category:

Biology (whole organism)

Subject Areas:

evolution/ecology/computational biology

Keywords:

animal seed dispersers, coexistence, glacial periods, multi-layer lattice model, tropical rainforests

Authors for correspondence:

Satoru Morita

e-mail: morita.satoru@shizuoka.ac.jp

Jin Yoshimura

e-mail: yoshimura.jin@shizuoka.ac.jp

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsos.150330> or via <http://rsos.royalsocietypublishing.org>.

The contribution of seed dispersers to tree species diversity in tropical rainforests

Satoshi Kakishima¹, Satoru Morita², Katsuhiko Yoshida³, Atsushi Ishida⁴, Saki Hayashi², Takahiro Asami⁵, Hiromu Ito¹, Donald G. Miller III⁶, Takashi Uehara¹, Shigeta Mori⁷, Eisuke Hasegawa⁸, Kenji Matsuura⁹, Eiti Kasuya¹⁰ and Jin Yoshimura^{1,2,11,12}

¹Graduate School of Science and Technology, and ²Department of Mathematical and Systems Engineering, Shizuoka University, Hamamatsu, Shizuoka 432-8561, Japan

³Biodiversity Conservation Planning Section, Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan

⁴Center for Ecological Research, Kyoto University, Otsu, Shiga 520-2113, Japan

⁵Department of Biology, Shinshu University, Matsumoto, Nagano 390-8621, Japan

⁶Department of Biological Sciences, California State University, Chico, CA 95929, USA

⁷Department of Food, Life, and Environmental Science, Faculty of Agriculture, Yamagata University, Tsuruoka, Yamagata 997-8555, Japan

⁸Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University, Sapporo, Hokkaido 060-8589, Japan

⁹Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

¹⁰Department of Biology, Faculty of Science, Kyushu University, Fukuoka 812-8581, Japan

¹¹Marine Biosystems Research Center, Chiba University, Kamogawa, Chiba 299-5502, Japan

¹²Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA

Tropical rainforests are known for their extreme biodiversity, posing a challenging problem in tropical ecology. Many hypotheses have been proposed to explain the diversity of tree species, yet our understanding of this phenomenon remains incomplete. Here, we consider the contribution of animal seed dispersers to the species diversity of trees. We built a multi-layer lattice model of trees whose animal seed dispersers

are allowed to move only in restricted areas to disperse the tree seeds. We incorporated the effects of seed dispersers in the traditional theory of allopatric speciation on a geological time scale. We modified the lattice model to explicitly examine the coexistence of new tree species and the resulting high biodiversity. The results indicate that both the coexistence and diversified evolution of tree species can be explained by the introduction of animal seed dispersers.

1. Introduction

Tropical rainforests are known for their extreme angiosperm diversity [1,2]: their biological richness exceeds that of any other plant community. Beginning in the 1970s, many hypotheses have been advanced to explain this high diversity [3–6]. Some of the hypotheses are based on ecological factors, such as seed predators, pathogens, seed banks, pollinators, light conditions, ant–plant interactions and seedling survival [7–23]. Among them, the negative density dependence of seedlings demonstrates the importance of seed predation, pathogens and seedling survival [19–24]. Other hypotheses reflect the statistical properties of migration and extinction [6,25,26]. Although there are many plausible causes of the extreme tree diversity of tropical rainforests, we still have no conclusive explanation of the mechanisms for the coexistence of so many tree species in tropical rainforests [1–3,6,26–28].

Among the ecological factors affecting tree species diversity, the importance of biotic interactions has been noted, especially mutualistic interactions [17,29–32]. Mutualism is a characteristic feature of tropical rainforests. Most tree species in tropical rainforests are angiosperms known to produce nectar and pollen in flowers attractive to insect and vertebrate pollinators and to bear fruit eaten by seed-dispersing animals [2]. Many intriguing cases of tight species-to-species mutualism are known in insects [8–10,29–34], e.g. a fig tree and its fig wasp, and orchids and their pollinators; the effects of pollinators and ant–tree interactions have been considered theoretically [18,33]. Angiosperm trees have been found to have relatively close relationships with specific seed dispersers, notably birds, bats and some other mammals [35–37], in mutualisms characterized as dispersal syndromes [38]. For example, some tree species yield a hard seed that can be broken and germinated only by elephants [39]. The importance of seed dispersers for the coexistence of tree species is well established [35–37,40,41]. Thus, the diversity of angiosperm tree species may originate from and is maintained by the mutualistic relationships of tree species and their pollinators and seed dispersers. Recent models explore the contribution of seed dispersers to tree diversity [42–46]. Here, we incorporate animal movements (paths) into a lattice space model.

We propose that the present extremely high diversity of tree species in tropical rainforests originates from tight mutualisms among angiosperm trees and their specific animal seed dispersers. In our model, we introduce species-specific animal movements for seed dispersal. These movements reduce competition among tree species. Because each animal species has a unique movement pattern [47–49], the dimensions of its habitat become uniquely species-specific [50,51]. Therefore, we may find an animal in one location, but never in another, even if the required habitat components are the same [52].

Geologically, tropical rainforests have experienced repeated fragmentations due to climatic oscillations [2,53–57]. Milankovich cycles and changes in the composition of the atmosphere have resulted in alternating glacial and interglacial periods, causing sea-level oscillations over approximately 120 m during the Cenozoic Era [58]. As a result, since the beginning of the Cenozoic Era, land areas (in particular, those supporting tropical rainforests) have been repeatedly fragmented by increasing sea levels during warm interglacial periods, then reunited by decreasing sea levels during cool glacial periods. Even on large continents such as those on which the Amazon and the African tropics occur, savannah communities predominated during glacial periods because of a decrease in precipitation [2,29,56]. During the glacial periods, rainforests were evidently separated and confined to small areas of each continent. These processes promoted speciation in many angiosperm tree lineages as well as in birds and insects. High species diversity in a community implies highly frequent speciation events and less frequent extinctions [57,59,60]. In this study, our models consider frequent allopatric speciation events due to repeated separations and reunifications of habitats caused by intermittent ice ages [61]. Allopatric speciation is assumed to have occurred in every mutualistic pair of a tree species and its partner. For example, if a single habitat were separated into three isolated areas twice, the total number of species would be $3^2 = 9$ tree species [57]. If a habitat were separated four times, then the total is $3^4 = 81$ tree species. Hence frequent geographical fragmentation is suggested as a core mechanism producing the high species diversity in many rainforest taxa [53,61].

Here, we build a lattice simulation model to incorporate the role of animal seed dispersers in the coexistence of tree species. We investigate whether the movements of animal seed dispersers affect tree species diversity and what characteristics of the movement of animals are important for the coexistence of tree species. In our basic model, we evaluate the effects of seed dispersers on the coexistence of tree species. In the extended evolutionary model, we incorporate the traditional theory of allopatric speciation by repeated fragmentation on a geological time scale to examine the promotion of species diversity.

2. Material and methods

2.1. Lattice model framework

Focusing on the mutualism between seed plants and their seed dispersers, we built a multi-layer lattice model of tree species with animal seed dispersers (figure 1*a,b*). All tree species grow in the plant layer of the lattice, while each animal has its own species-specific habitat and disperses the seeds of its partner within its habitat range in its own lattice layer. We assume species-specific patterns of seed dispersal by animal partners reduce interspecific competition among tree species, promoting their coexistence.

To verify the coexistence and persistence of tree species, we first built a $(n + 1)$ multi-layer lattice ecosystem model with n tree species (P_i for $i = 1, 2, \dots, n$) and their corresponding seed dispersers (A_i for $i = 1, 2, \dots, n$; figure 1*a,b*). The lattice size is 200×200 cells. The first layer is a plant layer (L_0), in which all tree species grow, and each animal species (A_i) moves within its own layer (L_i for $i = 1, 2, \dots, n$) to disperse seeds (figure 1*a*). Each cell in the plant layer (L_0) is either occupied by the i th tree species (P_i) or unoccupied (vacant: O_0). The seeds of a plant (P_i) are carried only by its animal partner (A_i) (figure 1*b*). The cells in an animal layer of the lattice are classified into two types: (i) cells where animals of species i can visit (either occupied or vacant: A_i or O_i , respectively) and (ii) cells where animals of species i cannot visit (unvisited site: U_i).

We evaluated the overall effects of the unvisited cells by varying their proportion in the animal lattice layers. As a control, we also built a single-layer lattice model without animals, where seeds were dispersed globally.

2.2. Specifications for the population model

To explore specifically the effects of animal–plant interactions on tree diversity, we introduced the following simplifications: animals are immortal with no reproduction, flowers are automatically pollinated to produce seeds and, after a seed is carried to a vacant cell, it will automatically grow to an adult tree, unless it dies (with a constant risk of mortality).

The process of seed dispersal and reproduction is as follows. In an animal layer (L_i), we pick a cell randomly. If the cell is occupied by an animal (A_i), we randomly choose one vacant cell (O_i) and move the animal to that cell, i.e. $A_i + O_i \rightarrow O_i + A_i$ (figure 1*b*). When the animal A_i moves, it carries and disperses the P_i seed if the animal was located above the cell where the P_i plant grows. If the seed is carried into a vacant cell, it automatically grows to an adult tree, i.e. $P_i + O_i \rightarrow O_i + P_i$ (figure 1*b*). Definitions of our symbols are given in table 1.

We varied the unvisited rates u of a plant species as follows. In the initial simulations, we set the unvisited rate u to be the same for all species. We varied the constant unvisited rate between 0 and 1 to examine its effects on the number of coexisting species. We also varied the unvisited rates of species to examine the superiority of species among species, such that $u_i = 1.0 - 0.1i$. We also considered the case when seed-dispersal mutualisms are not perfectly species-specific. When animal A_i moves to the cell where the P_j ($j \neq i$) plant grows, it carries and disperses the P_j seed with a decreased probability (20% or 50%).

A randomly chosen plant also dies at a constant mortality rate m_i , i.e. $P_i \rightarrow O_i$. Here, we make the species-specific mortality rates differ among species such that $m_i = 0.11 - 0.01i$ for $i = 1, \dots, 8$. The reason for this difference among species is to expedite simulation results. If we set the same mortality rate among all species, the simulation generates random walks in which the convergence time becomes excessively long. This species difference also makes the coexistence of species much less likely in the context of competitive interactions. We also examined the effects of mortality on the number of coexisting species and their density. Here, we keep the mortality of all species identical (the basic mortality $M = m_i$ for $i = 1, \dots, 8$), and the unvisited rates are varied among species such that $u_i = 1.0 - 0.1i$ for $i = 1, \dots, 8$.

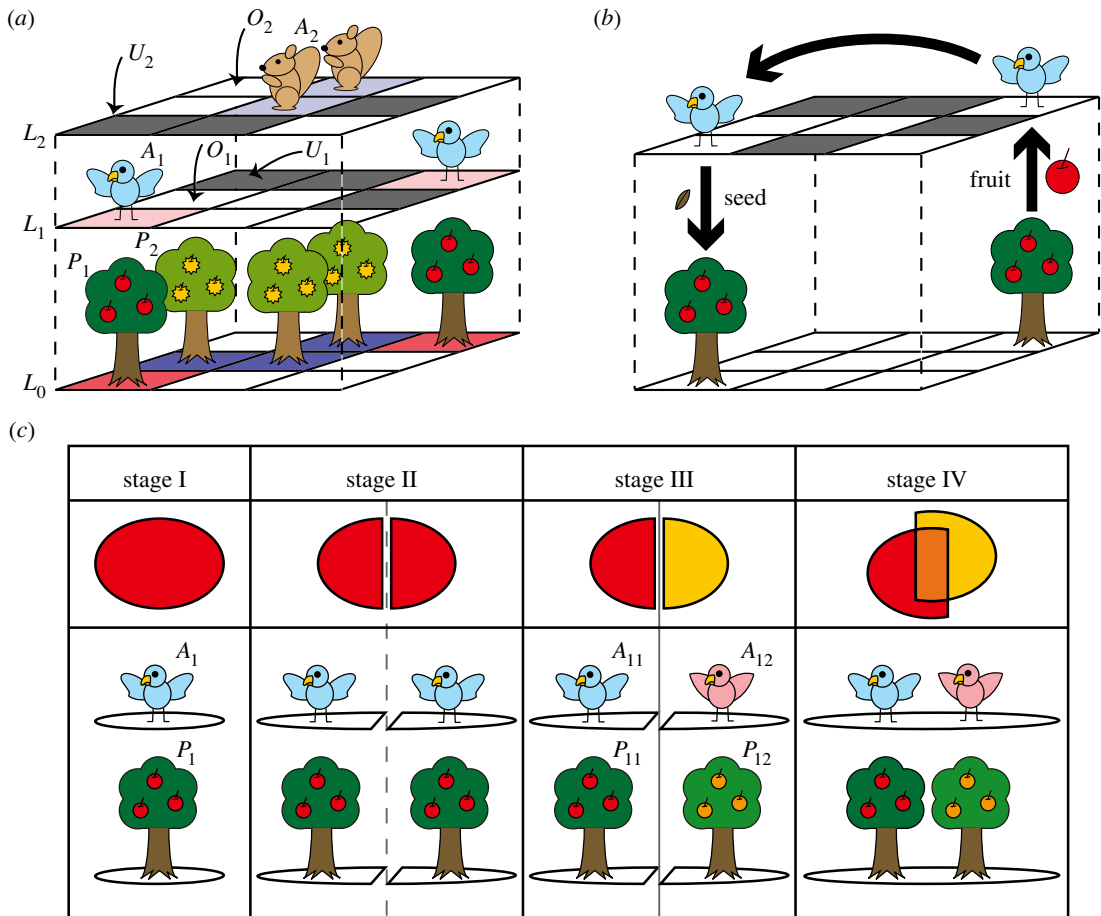


Figure 1. Schematic diagram of the population and evolution models. (a) Schematic diagram with two tree species (P_1 and P_2 on plant layer L_0) and the corresponding seed dispersers (birds A_1 on layer L_1 and squirrels A_2 on L_2). In each animal layer, the grey cells (U_1 and U_2) indicate unvisited sites (where animals never visit). (b) An animal (bird) eats a fruit (apple) at the tree (P_1) and drops a seed at an unoccupied site (O_1) that results in a new apple tree. (c) The fragmentation process repeats at every 6000 MCS, such that (stage I: a single habitat) \rightarrow 3000 MCS \rightarrow (stage II: habitat separation and stage III: species differentiation) \rightarrow 3000 MCS \rightarrow (stage IV: habitat reunification and resulting species coexistence = stage I).

Table 1. Glossary of symbols.

symbol	description
P_i	plant growth sites (cells). The subscript denotes species
A_i	sites visited by animals (cells). The subscript denotes species
L_i	layers. L_0 : a plant layer; L_1-L_n : animal layers for A_1-A_n
U_i	unvisited sites (cells). The subscript denotes species
O_i	unoccupied sites (cells). The subscripts denote either a layer, animal species, or both
u_i	unvisited rates. The subscript denotes species
m_i	mortality rates. The subscript denotes species
v	niche-shift probability

We performed this procedure for a given number of (Monte Carlo) steps. We set each Monte Carlo step (MCS) as 200×200 times. The initial densities of A_i and P_i are 0.1 for all population simulations. The template of a simulation program for the population model is provided in the electronic supplementary material, text S1.

2.3. Specifications for the evolutionary model

To simulate the evolutionary diversification of tree species, we applied repeated separations and unifications of habitats in the lattice model, where the separated trees and animal partners were assumed to evolve a new mutualistic relationship. The diversification of tree species was evaluated by the same lattice model by introducing repeated geographical isolations (figure 1c). The procedure consists of four stages: (I) the initial single-lattice habitat; (II) two isolated habitats; (III) the species differentiation stage, where each tree–animal system has diverged into two independent systems; and (IV) the habitat unification stage, where the isolated habitats are reunited into a single large habitat (=stage 1). This process approximates the evolutionary diversification of trees and their associated seed dispersers during repeated fragmentation by glacial periods on a geological time scale. A single large habitat before glaciation episodes (I) becomes isolated into two small isolated habitats when glaciation begins (II). During the glacial period (III), trees and their associated seed dispersers diverge into two distinct species. After the glacial period (IV), the two isolated habitats are united, owing to global warming during the following interglacial period. Geologic evidence indicates this process was repeated over many glacial periods during the Cenozoic Era [62], yielding the diversification of many animal and plant taxa [53,63,64]. We then evaluated the number of surviving species after the repeated fragmentations and unifications of the lattice space.

All the combinations of trees and animal dispersers are doubled during stage III when the habitat is separated. At stage II, the entire lattice is divided in half (200×100 cells). At stage III, we introduce speciation in all tree–animal interactions, i.e. a partnership ($P_i - A_i$ for $i = 1, 2, \dots, n$) \rightarrow two independent partnerships ($P_{ij} - A_{ij}$ and $P_{ij} - A_{ij}$ for $i = 1, 2, \dots, n$ and $j = 1, 2$, where j denotes an isolated habitat). Stage IV becomes Stage I of the next speciation cycle. After speciation begins, habitat modification occurs such that when the lattice space is divided in half, the distribution of the unvisited sites U_i is modified into two different distributions (U_{i1} and U_{i2}) in the following manner. The animals A_{ij} are resident in each half lattice ($j = 1, 2$), the unvisited cells U_{ij} in the j -lattice remain unmodified, while the unvisited cells U_{ik} ($k \neq j$) in the k -lattice are moved to its neighbouring cells with a niche-shift probability (v : described below), such that $U_{ij} + O_{ij} \rightarrow O_{ij} + U_{ij}$. Here, we modify the neighbouring cells in particular, because the niche shift of new species differs only slightly from habitat preferences compared with parental species (phylogenetic niche conservatism) [65,66]. If the selected cell is either an already unvisited cell or outside the boundary, movement to the cell is negated. If the niche-shift probability $v = 0$, then no speciation takes place, while a non-zero v means speciation with niche shift from the original habitat (visited cells). We set v as the same value among all species, assuming speciation is synchronized between trees and seed dispersers. Biotic interactions, such as host–mutualist and host–parasite interactions, are known to yield synchronized divergence patterns [34,67,68]. To explore temporal dynamics, we set $v = 10^{-2}$ for the initial simulation. To evaluate the effects of v and u , we set v between 10^{-2} and 10^{-5} for the current simulations. We varied the unvisited rates u of a species, as follows. In the initial evolutionary simulations, we set the unvisited rate $u = 0.8$ for all species. We also varied the constant unvisited rate between 0 and 1 to examine its effects on the number of coexisting species. When we evaluated the effects of niche-shift probability v , we set $u = 0.8, 0.6$ and 0.4 .

We start with three species and this fragmentation process is repeated three times: three plant species (P_i for $i = 1, 2, \dots, n$, where $n = 3$). Therefore, the total number of coexisting species if no extinction takes place becomes $3 \times 2 = 6$ species (P_{ij} for $j = 1, 2$) in a single iteration, $6 \times 2 = 12$ species (P_{ijk} for $j, k = 1, 2$) for two iterations, and $12 \times 2 = 24$ (P_{ijkl} for $j, k, l = 1, 2$) for three iterations. Initially, we set the species-specific mortality rates of three species, such that $m_i = 0.032 - 0.02i$ for $i = 1, 2, 3$ and all the derived species are assigned the same mortality rate as the parental species. The initial densities of A_i and P_i were 0.2 for all evolutionary simulations. The template of a simulation program for the evolutionary model is provided in the electronic supplementary material, text S2.

3. Results

The coexistence and persistence of species diversity was verified using a $(8 + 1)$ multi-layer lattice ecosystem model with eight tree species and their corresponding eight animal species for seed dispersal (figure 2). When there were no unvisited sites ($u = 0$), the tree species with the lowest mortality ($m_8 = 0.03$) excluded all other species immediately, occupying 80% of the lattice space (figure 2a). By contrast, when 80% of the lattice space consisted of unvisited sites ($u = 0.8$), all the tree species coexisted with less than a 0.2 steady-state density (figure 2b). In this case, the steady-state density of species depended on the mortality rate, such that superior species (species with a lower mortality rate) occurred

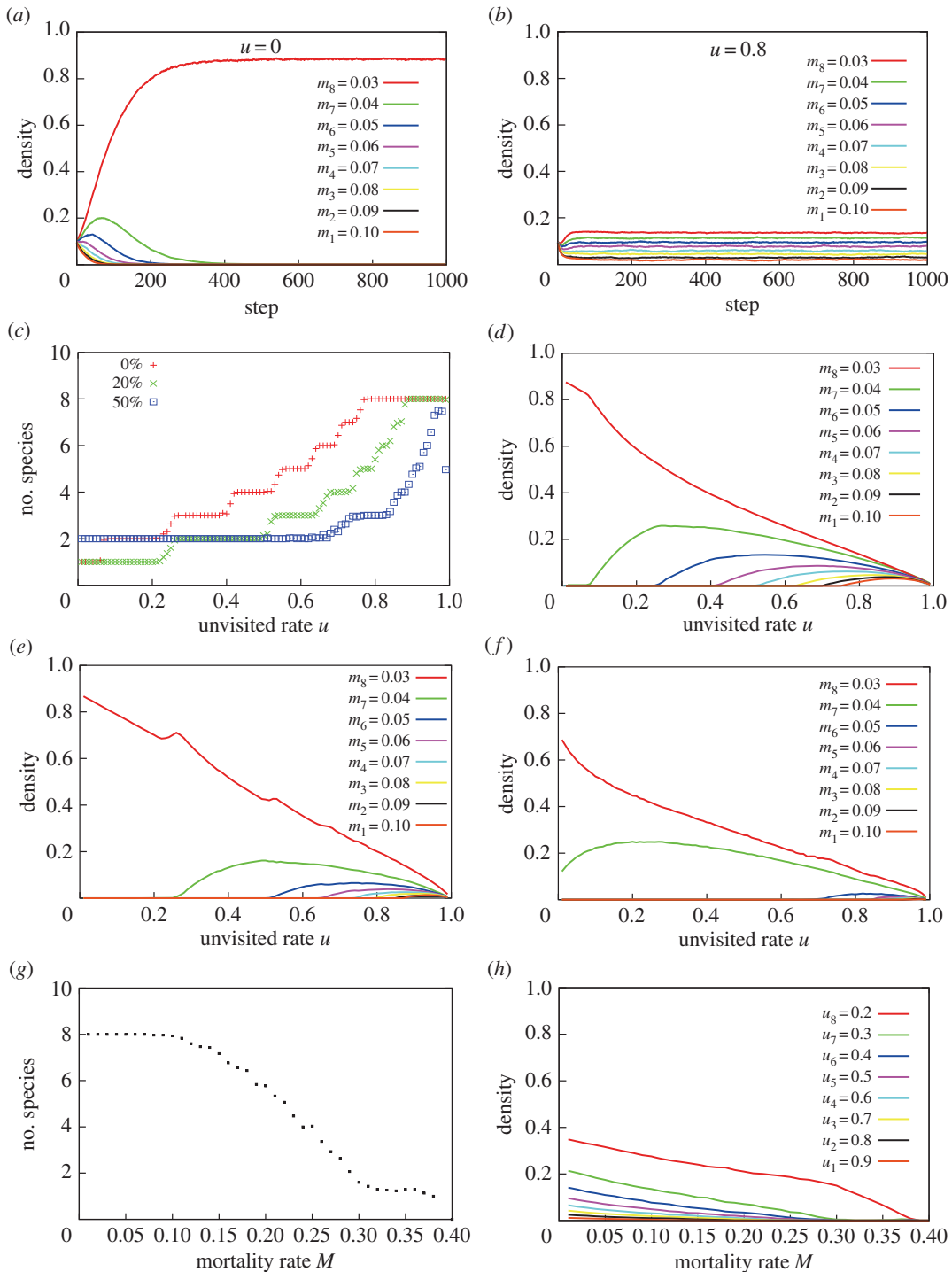


Figure 2. Persistence of eight tree species in the multi-layer lattice model of tropical rainforests. (a) Dynamics with no unvisited sites (unvisited rate: $u = 0$). (b) Dynamics with a high unvisited rate ($u = 0.8$). (c) The number of surviving species at steady state against u . (d–f) Steady-state densities against u , when the animal A_i carries and disperses the P_j ($j \neq i$) seed with (d) 0%, (e) 20% or (f) 50% probability. (g) The number of surviving species as a function of mortality rate $m_i = M$. (h) Steady-state densities against M . (a–f) Mortality rates of individual species are $m_i = 0.11 - 0.01i$. (c–h) Mean values of 30 trials. Steady-state density is estimated at 3000 MCS, because all simulation runs reach a steady state by 1000 MCS. (g,h) Unvisited rates of individual species are $u_i = 1.0 - 0.1i$. (a–h) The initial densities of A_i and $P_i = 0.1$. The drawing was created by S.H. and J.Y.

at high densities. Thus, coexistence of two or more tree species was nearly impossible when tree seeds were randomly dispersed ($u = 0$), while coexistence was guaranteed when the dispersal of tree seeds were highly restricted due to limited animal movements ($u = 0.8$). When seeds were dispersed globally without animals, the tree species with the lowest mortality rate ($m_8 = 0.03$) excluded all other species,

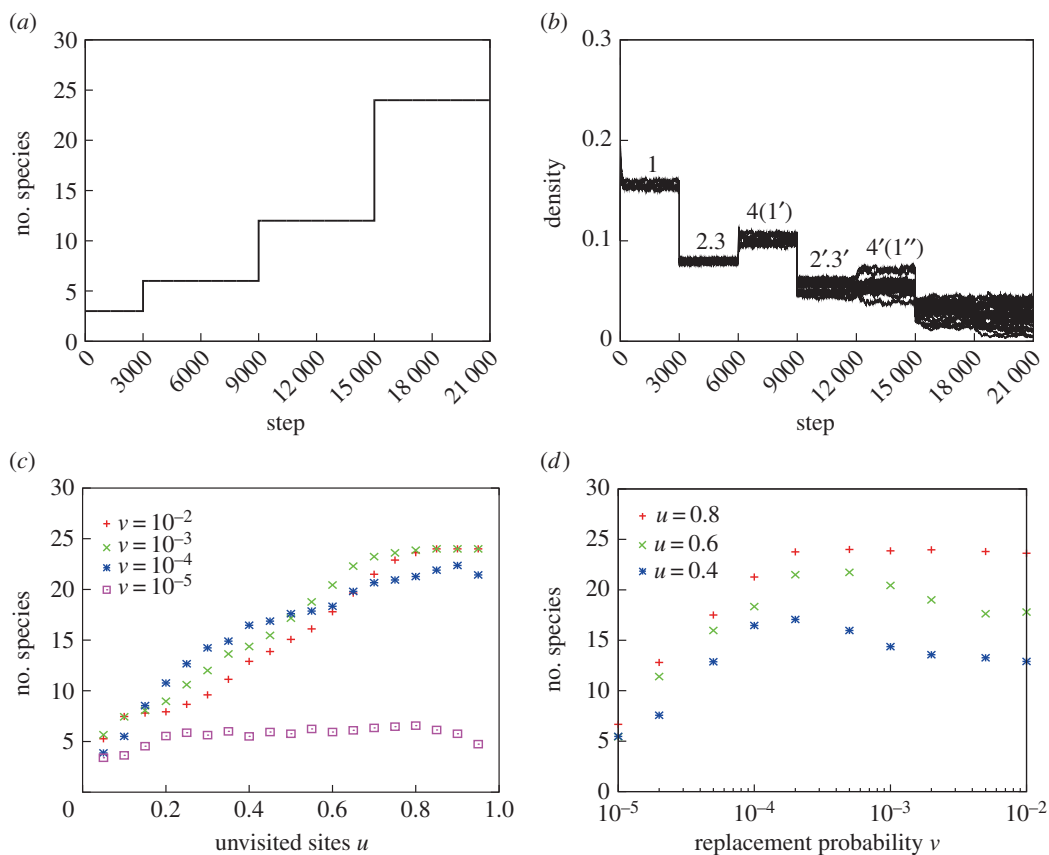


Figure 3. Diversification model via repeated habitat fragmentation in the multi-layer lattice model of tropical rainforests. (a) Dynamics of species diversity. (b) Density dynamics of all species. (c) The final number of species against the unvisited rate u for various levels of shift rate v in unvisited sites. With probability v , an unvisited site is shifted to a neighbouring cell ($v = 10^{-2}$, 10^{-3} , 10^{-4} and 10^{-5}). (d) The final number of species against the probability v for various u ($=0.4, 0.6$ and 0.8). (c,d) The averages of 30 trials were measured at 21 000 MCS. Parameters are: $m_1 = 0.03$, $m_2 = 0.028$ and $m_3 = 0.026$ and the initial densities of A_i and $P_i = 0.2$. The drawing was created by S.H. and J.Y.

which also occurred with animal dispersal with no unvisited sites ($u = 0$) (electronic supplementary material, figure S1).

We plotted the number and densities of tree species against the rates at which they were not visited ('unvisited') (figure 2c,d). When the unvisited rate increased, the number of coexisting species increased as a stepwise function, totalling eight species at about $u = 0.8$ (figure 2c). For the density of species, when the unvisited rate increased, the density of already existing species decreased, while newly coexisting species increased in density (figure 2d). When $u = 0.75$ – 0.99 , all eight species coexist with very low densities.

When the species specificity of seed dispersal is lower, the number of coexisting species decreases compared with perfect species-specificity (figure 2c). However, when the unvisited rate is high, the results are the same if animals can disperse the seeds of other plant species with a 20% probability. Even if this probability is increased to 50%, the number of coexisting species converges when the unvisited rate approaches unity. Thus, this mechanism is highly effective even if animal dispersers exhibit diminished species-specificity.

We plotted the number and densities of tree species against the basic mortality rates M (identical for all eight species), while the unvisited rates varied among species ($u_i = 1.0 - 0.1i$ for $i = 1, \dots, 8$). When the basic mortality rate was low ($M < 0.1$), all eight species coexisted (figure 2e). When mortality rates were further increased, the number of surviving species decreased rapidly, reaching only one species at approximately $M = 0.3$. As the basic mortality rate M increased, the densities of all species decreased (figure 2f). Here, a superior species remaining at a higher steady-state density always had a lower unvisited rate. Thus, species with a low unvisited rate always maintained a high density. However, coexistence became impossible when all animals moved freely to disperse seeds, i.e. $u = 0$ (figure 2c,d), or when the mortality rate was too high (figure 2e,f).

Figure 3 shows the simulation results for the diversified evolutionary model. Figure 3*a* shows the temporal dynamics of the number of coexisting species starting from three species ($m_i = 0.11 - 0.01i$, for $i = 1, 2, 3$), all with a 0.2 initial density with the unvisited rate $u = 0.8$ and the niche-shift probability $v = 10^{-2}$. With speciation events, the total number of coexisting species reached 24 species with no extinctions (figure 3*a*). The temporal dynamics of densities (figure 3*b*) showed a large reduction in density when the lattice space was fragmented into two halves because the number of species doubled (Stage II and III). Accordingly, when the fragmented lattices were reunited, the density of each species was increased.

We plotted the number of surviving species against the unvisited rate u for four different levels of the niche-shift probability v (10^{-2} , 10^{-3} , 10^{-4} and 10^{-5}) (figure 3*c*). When the niche-shift probability v was relatively large ($v = 10^{-2} - 10^{-3}$), no extinction occurred; this resulted in the maximum of 24 species as long as the unvisited ratio was high ($u > 0.8$). However, when v was smaller ($v = 10^{-4}$), extinctions occurred, resulting in fewer than 24 species, even if the unvisited ratio was sufficiently high ($u > 0.8$). Furthermore, when v was too small ($v = 10^{-5}$), the number of surviving species became close to the initial number of species.

To extend our analysis, we plotted the number of surviving species against the niche-shift probability v for three different levels of the unvisited rate (0.4, 0.6 and 0.8) (figure 3*d*). These plots reveal an optimal level of the niche-shift probability (v), indicating that the behavioural pattern of animals is critical for the coexistence of tree species; this trend became evident when $u = 0.4$ and 0.6.

4. Discussion

Our results indicate that the existence of habitat patches not visited by animal dispersers has an important role in the coexistence of species (figure 2). If there are no unvisited patches ($u = 0$), animals can move into any sites and deposit the seeds they carry, which is equivalent to random dispersal. In this case, one superior species immediately drives the others to extinction (figure 2*a*). By contrast, if there are many unvisited patches, some sites are likely to be almost exclusively available to one plant species, because of the limited access other species-specific animal dispersers have to these sites. In the extreme case, some sites are available to one animal species only, as the remaining animal species fail to visit these sites. Thus, each tree species occupies specific sites unavailable to the other tree species. Interestingly, the complete exclusion of seed dispersal appears unnecessary to promote coexistence of tree species. It is unknown how many species can coexist in the 40 000 sites (200×200 cells), but at least 24 species are possible in the current simulations (figure 3*a*).

Our model assumes many strict conditions, which may limit its general applicability to tropical rainforests. For example, our model assumes an exclusive one-to-one relationship between a tree species and its seed disperser. In reality, frugivorous animals are often considered generalists [69,70]. Because animals eat many types of fruit, they are likely to carry the seeds of other plants, albeit with lower probabilities. To explore this possibility, we ran the simulation with lowered relationship specificities. The results show that the coexistence of many species is still highly maintained, in spite of lower species specificity in seed dispersal (figure 2*c*). However, there remains a large gap between our assumptions and actual scenarios with frugivores.

Coexistence of multiple species, in our models, is achieved under the following necessary conditions: (i) there are mutualistic seed dispersers with specific movements (resulting in unvisited sites); (ii) the entire ecosystem (here, the whole lattice space) is divided and united repeatedly; (iii) when the ecosystem is divided into two or more patches, speciation occurs in both trees and their associated animal dispersers; and (iv) the changes in behavioural patterns and resulting dispersal sites should be neither too small nor too large. If the niche shift is too small, competitive exclusion takes place involving the parental species. If the niche shift is too large, then the unvisited sites of new animal species are distributed randomly. Thus, slight deviations from niches of the parental species seem important to promote coexistence of closely related species.

There is strong evidence that the fragmentation of distribution ranges results in the loss of diversity [71], probably because the likelihood of extinction increases when the ranges are small. Plant population sizes sufficient to avoid extinction are rather small in our models because the persistence of tree species is guaranteed by seed dispersers (figure 2). In our evolutionary model, fragmentation does not cause the extinction of all species because mutualistic seed dispersers prevent the competitive exclusion of tree species through the animals' unique dispersal behaviour (figure 3*a,b*). Moreover, the number of species may be increased exponentially by repeated fragmentation events.

Our hypothesis for extreme diversity in tropical rainforest trees incorporates two critical components: (i) mutualisms between animal seed dispersers and angiosperms and (ii) repeated geographical isolations during the Pleistocene. These elements occur in a unique historical context, where tropical rainforests are restricted to equatorial regions during glacial maxima [54,55]. While few hypotheses for rainforest tree diversity consider the importance of the historical backdrop, our hypothesis rests on assumptions explicitly addressing the biogeographic elements common to tropical rainforests generally [72].

Although our models provide theoretical support for the hypotheses that dispersal syndromes and range contractions promote speciation and the coexistence of tree species in the tropics, it ignores many important aspects of tropical rainforests, such as plant–pollinator mutualisms and phylogenetic constraints that act on trees and animal seed dispersers [29]. A more encompassing approach will necessarily consider the persistence and evolutionary branching patterns of mutualisms between angiosperm trees and their associated pollinators and seed dispersers. Tree phenology may also be important, as observed, for example, in mass fruiting events occurring in the Southeast Asian dipterocarp rainforests [73], as well as spatial limitations imposed by the complex plant architecture of the rainforest [72]. The population structure of seedlings probably reflects the movements of animal seed dispersers. These potential refinements may all affect the quantitative predictions of the nature of tree diversity, yet we expect our models to yield the same qualitative results. We find further support for our hypothesis in studies of the radiation of birds and insects in tropical regions [53,56,74,75]. Note that the extreme diversification of angiosperms in tropical rainforests evidently occurred over a fairly limited span in the Late Cenozoic, which was marked by abrupt cycles of glacial and interglacial periods over the past 2 Myr [76–78]. Our model may be expanded to include the plants with seeds spread by wind dispersal or gravity dispersal.

Our ecological simulation results imply that the coexistence of an extremely high number of tree species is possible in a relatively small geographical area (figure 2). Moreover, the results of the evolutionary simulation suggest that the final number of species depends mostly on repeated geographical isolations during the Pleistocene (figure 3). Here, the tropical forest region is separated and isolated into three or more areas, and the number of species becomes tripled or multiplied several times at each isolation event [57]. Hence the resulting number of species may be represented as n^m , where n represents the number of isolated habitat areas and m the number of isolation events. Our hypothesis is thus consistent with the pattern of explosive speciation documented in angiosperms in tropical forests [79–81].

There are two major classes of hypotheses explaining the extremely high species diversity of trees in tropical rainforests: (i) the niche hypotheses, such as the Janzen–Connell hypothesis [4,5,19–24], and (ii) the neutral theory of communities [6,26]. Our model can incorporate the negatively density-dependent properties inspiring the Janzen–Connell hypothesis [4,5,19–24], as follows. In the current model, animal movement is purely random; therefore, the distribution of each plant species is also random. However, animals often move away from trees where they harvest fruits. Furthermore, when animals release faeces that include fruit seeds, they may avoid (or are already distant from) the parental tree, thus seedlings are likely to be dispersed away from the natal trees. We should also note that the Janzen–Connell hypothesis itself may be incorporated into the current model. Seed mortality can be increased near the cells of parental trees in the current model. By incorporating the negative density effects of seedling survival, seed predation, pathogens and the species-specific animal dispersal of seedlings, we may approach a plausible explanation for the extreme high tree species diversity of tropical rainforests. The neutral theory of communities may act as an additional factor in the temporal diversity of tree species, reducing the extinction process of new tree species with their own partner animals [6,26].

Competition and coexistence are central to the origins and maintenance of extremely high levels of tree diversity in tropical rainforests. The theory of niche separation [7] indicates that, at most, only a few tree species can coexist in a single habitat. We suspect that all animal dispersers are distinguished by possession of unique niche separations; this quality, in turn, is expected to promote the coexistence of trees. Speciation of tree species can be achieved by a slight degree of differentiation in animal movements that guarantees the coexistence of closely related tree species (figure 3*c,d*). Hence, as long as these animals occupy distinctive niches, various tree species may be able to coexist in the same habitats. Thus the current theory is essentially a niche theory [4,5], not so much of plants but of animal mutualists. Similarly, coexistence is also impossible in a single-layer lattice model under global interactions (electronic supplementary material, figure S1). Thus, the coexistence and persistence of many tree species can be maintained by the presence of species-specific seed dispersers. We may expand this simple model to include the mortality of animal dispersers, tree species with wind and gravity dispersal,

such as Dipterocarpaceae, and the coevolution of insect pollinators to reach a more precise picture of the community biodiversity in tropical rainforests. We should stress that our model shows only one possible mechanism for extreme tree diversity and is limited by many strict conditions not necessarily applicable to tropical rainforests in general. We hope, however, that these ideas trigger various new approaches towards understanding species richness in tropical rainforests.

Data accessibility. The template of simulation programs is provided in the electronic supplementary material (Text S1 and S2).

Authors' contributions. S.K. conceived the study and wrote the manuscript; Sa.M. conceived the study, built the program for the model and ran the program; S.H. conceived the study and wrote the manuscript; K.Y. provided the interpretation of simulation data and revised the manuscript; A.I. provided the interpretation of simulation data and revised the manuscript; T.A. provided the interpretation of simulation data and revised the manuscript; H.I. built the program for the model and ran the program; D.G.M. provided the interpretation of simulation data and revised the manuscript; T.U. built the program for the model and ran the program; Sh.M. provided the interpretation of simulation data and revised the manuscript; E.H. provided the interpretation of simulation data and revised the manuscript; K.M. provided the interpretation of simulation data and revised the manuscript; E.K. provided the interpretation of simulation data and revised the manuscript; and J.Y. conceived the study and wrote the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This study was supported by the Asahi Glass Foundation (to S.K.) and Grants-in-Aid from the Japan Society for Promotion of Science (for JSPS fellows to S.K. and H.I., and no. 26840126 to S.K., no. 26400388 to Sa.M., nos. 24370009 and 26660125 to A.I., nos. 24255004 and 24370007 to T.A., no. 15K14746 to Sh.M., and nos. 22255004, 22370010, 26257405 and 15H04420 to J.Y.).

Acknowledgements. We thank Hideto Mori and Tomoaki Kikuchi for the development of the original version of the computer simulations and Yukiko Nariai for assistance in creating the drawing.

References

- Richards PW. 1996 *The tropical rain forest*, 2nd edn. Cambridge, UK: Cambridge University Press.
- Morley RJ. 2002 *Origin and evolution of tropical rain forests*. Chichester, UK: John Wiley and Sons.
- Wright SJ. 2002 Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**, 1–14. (doi:10.1007/s004420100809)
- Janzen DH. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–529. (doi:10.1086/282687)
- Connell JH. 1971 On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (eds Den Boer PJ, Gradwell G), pp. 298–312. Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation.
- Hubbell SP. 1979 Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**, 1299–1309. (doi:10.1126/science.203.4387.1299)
- Terborgh J. 1973 On the notion of favorableness in plant ecology. *Am. Nat.* **107**, 481–501. (doi:10.1086/282852)
- Johnson SD, Steiner KE. 2000 Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15**, 140–143. (doi:10.1016/S0169-5347(99)01811-X)
- Bernhardt P. 2000 Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Plant Syst. Evol.* **222**, 293–320. (doi:10.1007/BF00984108)
- Ghazoul J. 2005 Pollen and seed dispersal among dispersed plants. *Biol. Rev.* **80**, 413–443. (doi:10.1017/S1464793105006731)
- Takenaka A. 2006 Dynamics of seedling populations and tree species coexistence in a forest: a simulation study. *Ecol. Res.* **21**, 356–363. (doi:10.1007/s1284-006-0165-y)
- Kohyama TS, Takada T. 2009 The stratification theory for plant coexistence promoted by one-sided competition. *J. Ecol.* **97**, 463–471. (doi:10.1111/j.1365-2745.2009.01490.x)
- Kohyama TS, Takada T. 2012 One-sided competition for light promotes coexistence of forest trees that share the same adult height. *J. Ecol.* **100**, 1501–1511. (doi:10.1111/j.1365-2745.2012.02029.x)
- Brown C *et al.* 2013 Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proc. R. Soc. B* **280**, 20130502. (doi:10.1098/rspb.2013.0502)
- Sterck F, Markesteijn L, Schieving F, Poorter L. 2011 Functional traits determine trade-offs and niches in a tropical forest community. *Proc. Natl Acad. Sci. USA* **108**, 20 627–20 632. (doi:10.1073/pnas.1106950108)
- McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006 Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185. (doi:10.1016/j.tree.2006.02.002)
- Mittelbach G *et al.* 2007 Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10**, 315–331. (doi:10.1111/j.1461-0248.2007.01020.x)
- Duthie AB, Falcy MR. 2013 The influence of habitat autocorrelation on plants and their seed-eating pollinators. *Ecol. Model.* **251**, 260–270. (doi:10.1016/j.ecolmodel.2012.12.019)
- Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA. 2000 Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**, 493–495. (doi:10.1038/35006630)
- Peters HA. 2003 Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecol. Lett.* **6**, 757–765. (doi:10.1046/j.1461-0248.2003.00492.x)
- Bagchi R, Swinfield T, Gallery RE, Lewis OT, Gripenberg S, Narayan L, Freckleton RP. 2010 Testing the Janzen–Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecol. Lett.* **13**, 1262–1269. (doi:10.1111/j.1461-0248.2010.01520.x)
- Johnson DJ, Beaulieu WT, Bever JD, Clay K. 2012 Conspecific negative density dependence and forest diversity. *Science* **336**, 904–907. (doi:10.1126/science.1220269)
- Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, Freckleton RP, Lewis OT. 2014 Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88. (doi:10.1038/nature12911)
- Jansen PA, Visser MD, Wright JS, Rutten G, Muller-Landau HC. 2014 Negative density dependence of seed dispersal and seedling recruitment in a neotropical palm. *Ecol. Lett.* **17**, 1111–1120. (doi:10.1111/ele.12317)
- Volkov I, Banavar JR, Hubbell SP, Maritan A. 2003 Neutral theory and relative species abundance in ecology. *Nature* **424**, 1035–1037. (doi:10.1038/nature01883)
- Hubbell SP. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
- Chesson P. 2000 Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366. (doi:10.1006/tpbi.2000.1486)
- Chisholm RA, Pacala SW. 2010 Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proc. Natl Acad. Sci. USA* **107**, 15 821–15 825. (doi:10.1073/pnas.1009387107)

29. Whitmore TC. 1998 *An introduction to tropical rain forests*, 2nd edn. Oxford, UK: Oxford University Press.
30. Herre EA, Jander KC, Machado CA. 2008 Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annu. Rev. Ecol. Syst.* **39**, 439–458. (doi:10.1146/annurev.ecolsys.37.091305.110232)
31. Kato M, Kosaka Y, Kawakita A, Okuyama Y, Kobayashi C, Phimminith T, Thongphan D. 2008 Plant–pollinator interactions in tropical monsoon forests in Southeast Asia. *Am. J. Bot.* **95**, 1375–1394. (doi:10.3732/ajb.0800114)
32. Kaiser-Bunbury CN, Memmott J, Muller CB. 2009 Community structure of pollination webs of Mauritian heathland habitats. *Perspect. Plant Ecol.* **11**, 241–254. (doi:10.1016/j.ppees.2009.04.001)
33. Céréghino R, Leroy C, Dejean A, Corbara B. 2010 Ants mediate the structure of phytotelm communities in an ant-garden bromeliad. *Ecology* **91**, 1549–1556. (doi:10.1890/09-1534.1)
34. Yokoyama J. 1995 Insect–plant coevolution and speciation. In *Biodiversity and evolution* (eds Arai R, Kato M, Doi Y), pp. 115–130. Tokyo, Japan: The National Science Museum Foundation.
35. Janzen DH, Martin PS. 1982 Neotropical anachronisms: the fruits the gomphotheres ate. *Science* **215**, 19–27. (doi:10.1126/science.215.4528.19)
36. Lomascolo SB, Levey DJ, Kimball RT, Bolker BM, Alborn HT. 2010 Dispersers shape fruit diversity in *Ficus* (Moraceae). *Proc. Natl Acad. Sci. USA* **107**, 14 668–14 672. (doi:10.1073/pnas.1008773107)
37. Klinger R, Rejmanek M. 2010 A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia* **162**, 951–963. (doi:10.1007/s00442-009-1542-3)
38. van der Pijl L. 1969 *Principles of dispersal in higher plants*. Berlin, Germany: Springer.
39. Blake S, Deem SL, Mossimbo E, Maisels F, Walsh P. 2009 Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468. (doi:10.1111/j.1744-7429.2009.00512.x)
40. Seidler TG, Plotkin JB. 2006 Seed dispersal and spatial pattern in tropical trees. *PLoS Biol.* **4**, e344. (doi:10.1371/journal.pbio.0040344)
41. Donatti CI, Guimarães PR, Galetti M, Pizo MA, Marquitti FMD, Dirzo R. 2011 Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecol. Lett.* **14**, 773–781. (doi:10.1111/j.1461-0248.2011.01639.x)
42. Levine JM, Murrell DJ. 2003 The community-level consequences of seed dispersal patterns. *Annu. Rev. Ecol. Syst.* **34**, 549–574. (doi:10.1146/annurev.ecolsys.34.011802.132400)
43. Nathan R, Casagrandi R. 2004 A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen–Connell and beyond. *J. Ecol.* **92**, 733–746. (doi:10.1111/j.0022-0477.2004.00914.x)
44. Muller-Landau HC. 2007 Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica* **39**, 372–384. (doi:10.1111/j.1744-7429.2007.00290.x)
45. Muller-Landau HC, Adler FR. 2007 How seed dispersal affects interactions with specialized natural enemies and their contribution to the maintenance of diversity. In *Seed dispersal: theory and its application in a changing world* (eds AJ Dennis, EW Schupp, RJ Green, DA Westcott), pp. 407–426. Wallingford, UK: CAB International.
46. Muller-Landau HC, Wright SJ, Calderón O. 2008 Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**, 653–667. (doi:10.1111/j.1365-2745.2008.01399.x)
47. Worton BJ. 1987 A review of models of home range for animal movement. *Ecol. Mod.* **38**, 277–298. (doi:10.1016/0304-3800(87)90101-3)
48. Vanleeuwé H, Gautier-Hion A. 1998 Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forests. *Afr. J. Ecol.* **36**, 174–182. (doi:10.1046/j.1365-2028.1998.00123.x)
49. De Luca DW, Pictou Philipps G, Machaga SJ, Davenport TRB. 2010 Home range, core areas and movement in the ‘critically endangered’ kipunji (*Rungwecebus kipunji*) in southwest Tanzania. *Afr. J. Ecol.* **48**, 895–904. (doi:10.1111/j.1365-2028.2009.01189.x)
50. Greenwood PJ, Harvey PH. 1982 The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**, 1–21. (doi:10.1146/annurev.es.13.110182.000245)
51. Luiselli L. 2007 Nonrandom co-occurrence patterns of rainforest chameleons. *Afr. J. Ecol.* **45**, 336–346. (doi:10.1111/j.1365-2028.2006.00715.x)
52. Elton CS. 1949 Population interspersal: an essay on animal community patterns. *J. Ecol.* **37**, 1–23. (doi:10.2307/2256726)
53. Haffer J. 1969 Speciation in Amazonian forest birds. *Science* **165**, 131–137. (doi:10.1126/science.165.3889.131)
54. Colinvaux PA, Liu K-B, de Oliveira P, Bush MB, Miller MC, Kannan MS. 1996 Temperature depression in the lowland tropics in glacial times. *Clim. Change* **32**, 19–33. (doi:10.1007/BF00141276)
55. Gates DM. 1993 *Climatic change and its biological consequences*. Sunderland, MA: Sinauer.
56. Prance GT. 1981 Discussion of aspects of Neotropical bird speciation during the Cenozoic. In *Vicariance biogeography: a critique* (eds G Nelson, DE Rosen), pp. 395–405. New York, NY: Columbia University Press.
57. Tainaka K, Itoh Y, Yoshimura J, Asami T. 2006 A geographic model of high species diversity. *Popul. Ecol.* **48**, 113–119. (doi:10.1007/s10144-006-0258-z)
58. IPCC. 2001 *Climate change 2001: the scientific basis, working group I*. Cambridge, UK: Cambridge University Press.
59. Yoshimura J, Stamer WT. 1997 Speciation and evolutionary dynamics of asymmetric mating preference. *Res. Popul. Ecol.* **39**, 191–200. (doi:10.1007/BF02765265)
60. Kawata M, Yoshimura J. 2000 Speciation by sexual selection in hybridizing populations without viability selection. *Evol. Ecol. Res.* **2**, 897–909.
61. Qian H, Ricklefs RE. 2000 Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature* **407**, 180–182. (doi:10.1038/35025052)
62. Benn D, Evans DJA. 2010 *Glaciers and glaciation*, 2nd edn. New York, NY: Routledge.
63. Richardson JE, Pennington R, Pennington TD, Hollingsworth PM. 2001 Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science* **293**, 2242–2245. (doi:10.1126/science.1061421)
64. Hewitt GM. 2004 Genetic consequences of climatic oscillations in the Quaternary. *Phil. Trans. R. Soc. Lond. B* **359**, 183–195. (doi:10.1098/rstb.2003.1388)
65. Wiens JJ, Graham CH. 2005 Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.* **36**, 519–539. (doi:10.2307/30033815)
66. Losos JB. 2008 Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**, 995–1003. (doi:10.1111/j.1461-0248.2008.01229.x)
67. Mitter C, Brooks DR. 1983 Phylogenetic aspects of evolution. In *Coevolution* (eds DJ Futuyma, M Slatkin), pp. 65–98. Sunderland, MA: Sinauer Associates Inc.
68. Vienne DM, Réfrégier G, López Villavicencio M, Tellier A, Hood ME, Giraud T. 2013 Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. *New Phytol.* **198**, 347–385. (doi:10.1111/nph.12150)
69. Bascompte J, Jordano P, Olesen JM. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433. (doi:10.1126/science.1123412)
70. Bascompte J, Jordano P. 2007 Plant–animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Syst.* **38**, 567–593. (doi:10.1146/annurev.ecolsys.38.091206.095818)
71. Turner IM. 1996 Species loss in fragments of tropical rain forest: a review of the evidence. *J. Appl. Ecol.* **33**, 200–209. (doi:10.2307/2404743)
72. MacArthur RH. 1972 *Geographical ecology: patterns in the distribution of species*. Princeton, NJ: Princeton University Press.
73. Appanah S. 1985 General flowering in the climax rain forests of South-east Asia. *J. Trop. Ecol.* **1**, 225–240. (doi:10.1017/S0266467400003004)
74. Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD. 2006 Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**, 1115–1118. (doi:10.1126/science.1129237)
75. Dyer LA *et al.* 2007 Host specificity of Lepidoptera in tropical and temperate forests. *Nature* **448**, 696–699. (doi:10.1038/nature05884)
76. Esat TM, McCulloch MT, Chappell J, Pillans B, Omura A. 1999 Rapid fluctuations in sea level recorded at the Huon Peninsula during the penultimate deglaciation. *Science* **283**, 197–201. (doi:10.1126/science.283.5399.197)
77. Plana V. 2004 Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. *Phil. Trans. R. Soc. Lond. B* **359**, 1585–1594. (doi:10.1098/rstb.2004.1535)
78. Burnham RJ, Johnson KR. 2004 South American palaeobotany and the origins of neotropical rainforests. *Phil. Trans. R. Soc. Lond. B* **359**, 1595–1610. (doi:10.1098/rstb.2004.1531)
79. Axelrod DI. 1952 A theory of angiosperm evolution. *Evolution* **6**, 29–60. (doi:10.2307/2405502)
80. van der Hammen T. 1974 The Pleistocene changes of vegetation and climate in tropical South America. *J. Biogeogr.* **1**, 3–26. (doi:10.2307/3038066)
81. Raven PH, Axelrod DI. 1974 Angiosperm biogeography and past continental movements. *Ann. MO Bot. Gard.* **61**, 539–573. (doi:10.2307/2395021)