

— Course Report “Ecological Modelling” —

# A Simple Janzen-Connell Model

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The Janzen-Connell Hypothesis posits that density-dependent seed mortality rates, as may be caused by pathogens or predators, can help maintain high levels of diversity in a tree community. Here, I present a spatially explicit, individual-based, forest community model to test the predictions of the this and several related hypotheses. As predicted by theory, the Janzen-Connell effect appears when the pathogen infection radius is less than the seed dispersal distance, and disappears once it becomes greater. Overall, however, the presence or absence of competitive exclusion has the strongest effect on species diversity.

## 1 Introduction

One of the most fundamental patterns of biogeography is the existence of strong latitudinal diversity gradients in many taxa. Tropical forests in particular are known for harbouring extraordinarily high levels of species richness of trees and other organisms. Explaining the mechanisms that originated and sustain this diversity has long been a key topic in ecological research (Wright, 2002; Cox et al., 2016).

Traditionally, many questions about species distributions were attributed to the results of interspecific competition. However, in the early 1970s, Daniel Janzen and Joseph Connell independently proposed an hypothesis linking the observed tree diversity to predation pressure (Janzen, 1970; Connell, 1971). They pointed out that seed dispersal broadly follows an exponential distribution, with most seeds falling close to the parent and only few being scattered further. However, they noted, seed mortality was highest in the parent’s vicinity—thus, effective population recruitment followed a hump-shaped pattern around the parent tree (fig. 1). This, they said, explained why conspecific trees

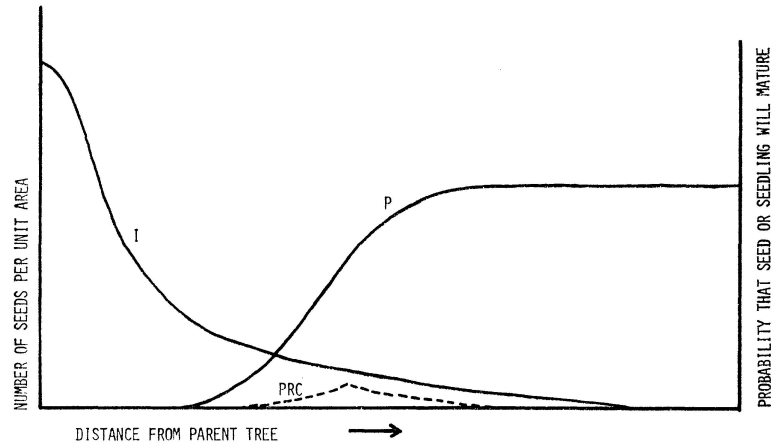


Figure 1: Janzen's original figure explaining the effect.  $I$  is the seed density,  $P$  the survival probability,  $PRC$  the population recruitment curve (from Janzen, 1970).

in tropical forests are so widely and evenly spread out, enabling the persistence of high diversity levels.

Since then, their proposed effect has been much studied, and has been generally confirmed (Comita et al., 2014). Predation by insects and the actions of (especially soil) pathogens are now known to be the main relevant causes for seed and seedling mortality (Wright, 2002). The relevance of the effect has also been found to extend beyond the tropics into temperate zones (Petermann et al., 2008); and it appears to even apply below the species boundary to individual populations (Liu et al., 2012).

However, the Janzen-Connell effect does not apply under all circumstances, and this too has been hotly discussed in the literature (e.g. Nathan and Casagrandi, 2004). For one, empirical evidence shows that its strength can vary strongly between different habitat types, and between species, depending on life-history strategies and growth form (Comita et al., 2014).

On a theoretical level, Hubbell (1980) criticised the lack of quantitative measures in Janzen's graphs. He argued that seed production was great enough to effectively swamp predators, and that recruitment therefore largely did follow dispersal. McCanny (1985) expanded on these thoughts, showing that a number of other recruitment patterns were at least theoretically possible, including a scenario in which survival stays constant or decreases with distance to the parent (see the comparison in fig. 2).

Aside from the magnitude of seed production or predation, the relative distances of seed and predator dispersal is also important. Nathan and Casagrandi (2004) showed mathematically that the Janzen-Connell effect can only manifest where the mean seed dispersal distance is greater than the mean movement/infection range of predators or pathogens. If the dispersal distance is equal to or less than the predation distance, they

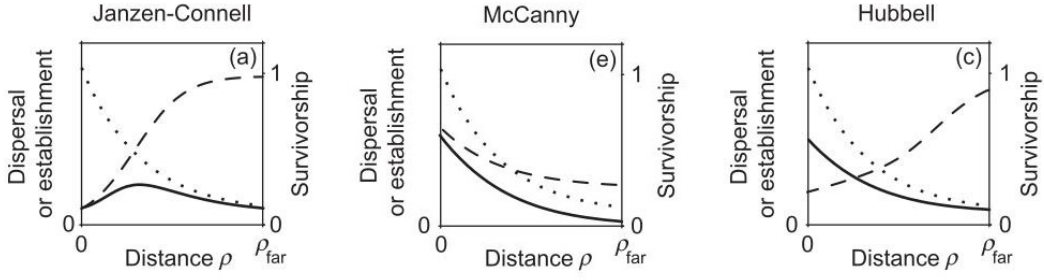


Figure 2: Different models of tree recruitment patterns. Dotted line: dispersal curve; dashed line: survivorship; solid line: establishment/effective recruitment (modified from Nathan and Casagrandi, 2004).

show, the Hubbell or McCann patterns exert themselves instead.

Here, I explore the effects of competition, pathogens, and dispersal distances on tree diversity using an individual-based forest community model. This modelling approach is useful for gaining a mechanistic understanding of complex systems, and has been successfully applied in a number of forest models (Grimm and Railsback, 2005). Whereas the ordinary differential equations employed by Nathan and Casagrandi modelled only the dispersal properties of a single tree, the model described herein can simulate not just the interactions of numerous individuals, but multiple species, too; resulting in a more realistic and reliable replication of the natural system under study.

Altogether, I modelled four different scenarios. Scenario 1, the control, represented a null model based on the neutral theory of ecology (Hubbell, 2001). In line with the theory’s assumption of functional equivalence, all species’ trait values were kept identical (Hubbell, 2005). Scenario 2 added the possibility of competitive exclusion by randomly varying species’ default trait values (and consequently their evolutionary fitness). Pathogens were only introduced in scenarios 3 and 4. For the third scenario, the pathogen infection radius was less than the tree’s average dispersal radius (“low transmission”), and should therefore lead to a Janzen-Connell recruitment pattern. The fourth scenario had equal infection and dispersal radii (“high transmission”), and should thus produce a Hubbell pattern (fig. 2).

## 2 Materials and Methods

I constructed an individual-based model simulating 16 tree species growing in a 1 km<sup>2</sup> forest patch, implemented with continuous space and discrete time. The model was implemented in Julia (Bezanson et al., 2017) and analysed with R and `ggplot2` (Wickham, 2016; R Core Team, 2020). All software source code and accompanying documentation may be downloaded from <https://github.com/veddox/jcm>.

The model involved three different entity types: species, trees, and pathogens. Each

Table 1: Overview of model entities with their traits and default trait values. Tree defaults refer to a freshly planted seed. Blank defaults indicate properties that must be specified on a per-instance basis.

<b>Species</b>		<b>Tree</b>		<b>Pathogen</b>	
<i>Trait</i>	<i>Default</i>	<i>Trait</i>	<i>Default</i>	<i>Trait</i>	<i>Default</i>
id		uid		host	
max_age	150	species		infectious	false
max_size	25	age	0	infection_rate	0.8
growth_rate	2	size	1	infection_radius	40/200
seed_production	10	mature	false	lethality	0.05
dispersal_distance	200	infection	nothing		
pathogen_resistance	0	position			

Table 2: List of ecological processes simulated by the model, in their order of execution.

<b>Process</b>	<b>Explanation</b>
<i>Dispersal</i>	Mature trees produce seeds that are randomly distributed and planted within the trees’ dispersal distance, using a uniform density distribution.
<i>Competition</i>	Each tree is checked for overlap with neighbouring trees. If two trees overlap, the smaller one is killed.
<i>Infection</i>	Infected trees pass on their pathogen to conspecifics in the neighbourhood, after an incubation period of one update. The probability of a successful infection depends on the distance to the infectious tree, the pathogen’s infection rate and the recipient tree’s resistance. Infected trees have an added per-update mortality probability given by the pathogens lethality.
<i>Growth</i>	Trees increase in size until they reach their species’ maximum size. Individuals that reach their species’ maximum age die.

individual tree was assigned a species, which determined its life-history trait values. Trees could also be infected by species-specific pathogens. Each entity type’s traits and their default values are listed in table 1.

The core submodel, simulating the trees’ life cycle, included the processes dispersal, competition, and growth. A second submodel added the epidemiological dimension, modelling pathogens with their transmission and lethality. A chronological listing and further explanation of these processes can be found in table 2.

A model run was initialised with one individual tree of each species scattered in the landscape. Each individual had its size set to its species’ **max\_size** and its age to half the species’ **max\_age**, ensuring that all were mature and could reproduce in the first update. Each simulation ran for 1000 updates, or approximately six generations.

In scenarios including interspecific competition, species’ default trait values were ran-

domly varied in the range of  $\pm 50\%$ . Pathogen introductions in scenarios 3 and 4 happened at initialisation by infecting all trees with their host-specific pathogen.

During a run, the model recorded every individual tree's trait values every 50 updates, and saved these to a CSV file for analysis. They were used to plot map time series of the simulation forest and to calculate population density, Shannon's diversity, and equitability over time for each individual run (Begon et al., 2006). A whole-experiment analysis was carried out by comparing the final distribution of species richness, range sizes, population density, and relative population size across all scenarios and replicates. I did not test for statistical significance, as such tests are unsuited to the context of simulation models (White et al., 2014).

### 3 Results

As an illustration of model behaviour, fig. 3 depicts an exemplary time series of maps of the simulation arena. It shows the development from initialisation, through the range expansion phase, into quasi-equilibrium in the late simulation.

Visual inspection of individual runs generally showed a sharp initial drop in diversity, followed by a steady, though not always monotonic, further decline (data not shown). In some runs, all 16 species survived to the end. In most cases, a quasi-equilibrium was reached over the course of the run.

In the whole-experiment analysis, the neutral scenario (1) had much higher species richness levels than the scenarios with interspecific competition (2-4), as shown in fig. 4. Fig. 5 shows the remaining diversity and evenness measures for all species across all scenarios; namely the population range size (in hectares), the in-range population density (individuals per hectare), and the relative population size (percent of the community size).

## 4 Discussion

### 4.1 Effect of competition and pathogens on diversity

The most noticeable result in this experiment is the large difference between the neutral scenario and those experiencing asymmetric interspecific competition. Scenario 1 not only had the highest average species richness and largest population ranges, but also a generally low population density; all of which are hallmarks of highly diverse systems like tropical rainforests. This may be taken in support of Hubbell's neutral theory (Hubbell, 2001), at least as far as its theoretical plausibility is concerned. The contrasting low species richness of scenarios 2-4 appear to be the result of competitive exclusion, with an added effect from pathogen-induced extinction for scenario 4.

As stated in the introduction, a Janzen-Connell recruitment pattern was expected for scenario 3 (low transmission). Indeed, this scenario showed slightly higher species survival and lower population densities (i.e. higher diversity) than the other two competitive

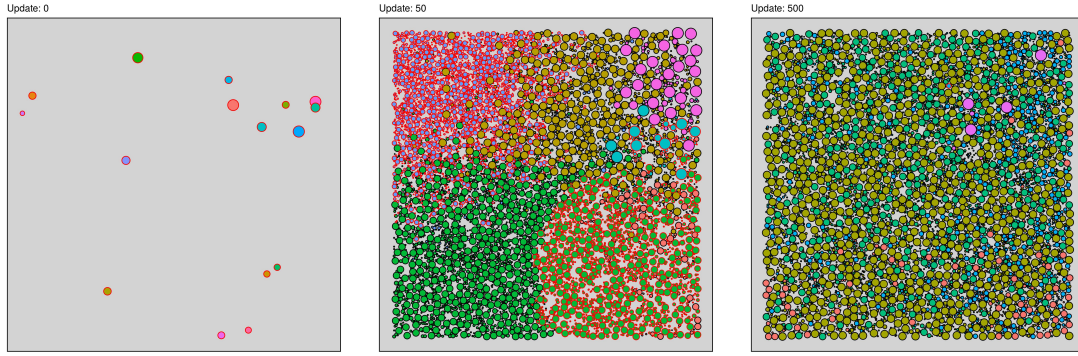


Figure 3: Model maps from an example run (low transmission scenario, replicate 0) after initialisation, at 50, and at 500 updates. Circles are individual trees, fill colours denote species. Trees with a red border are infected.

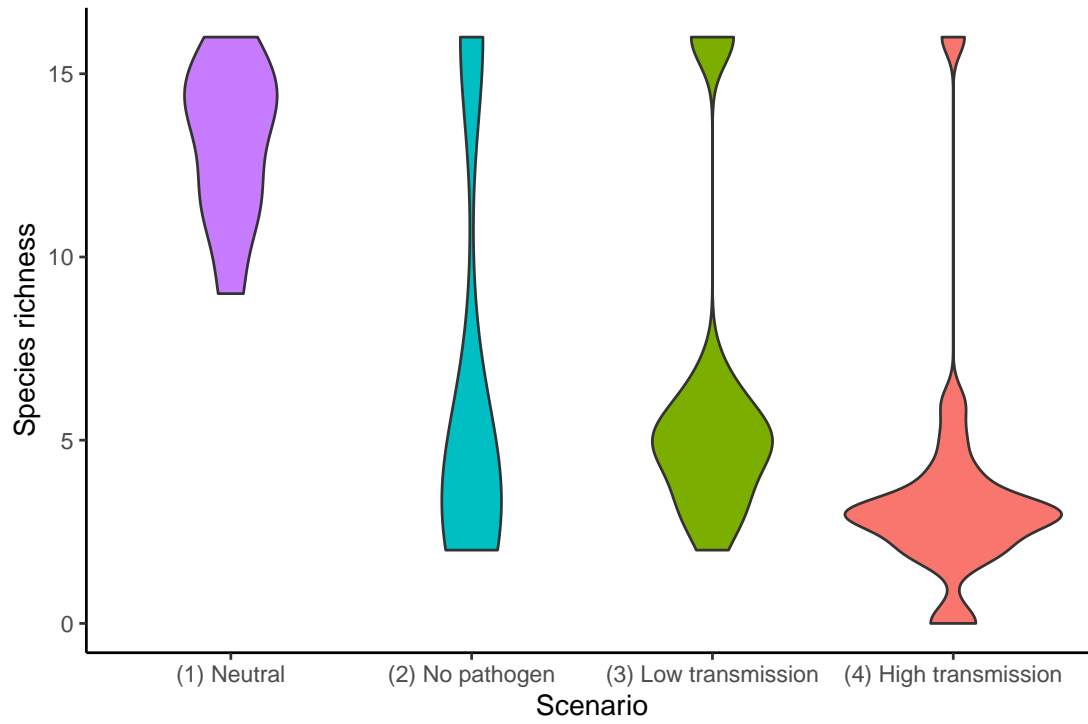


Figure 4: Number of species surviving to the end of the simulation in each scenario (20 replicates per scenario).

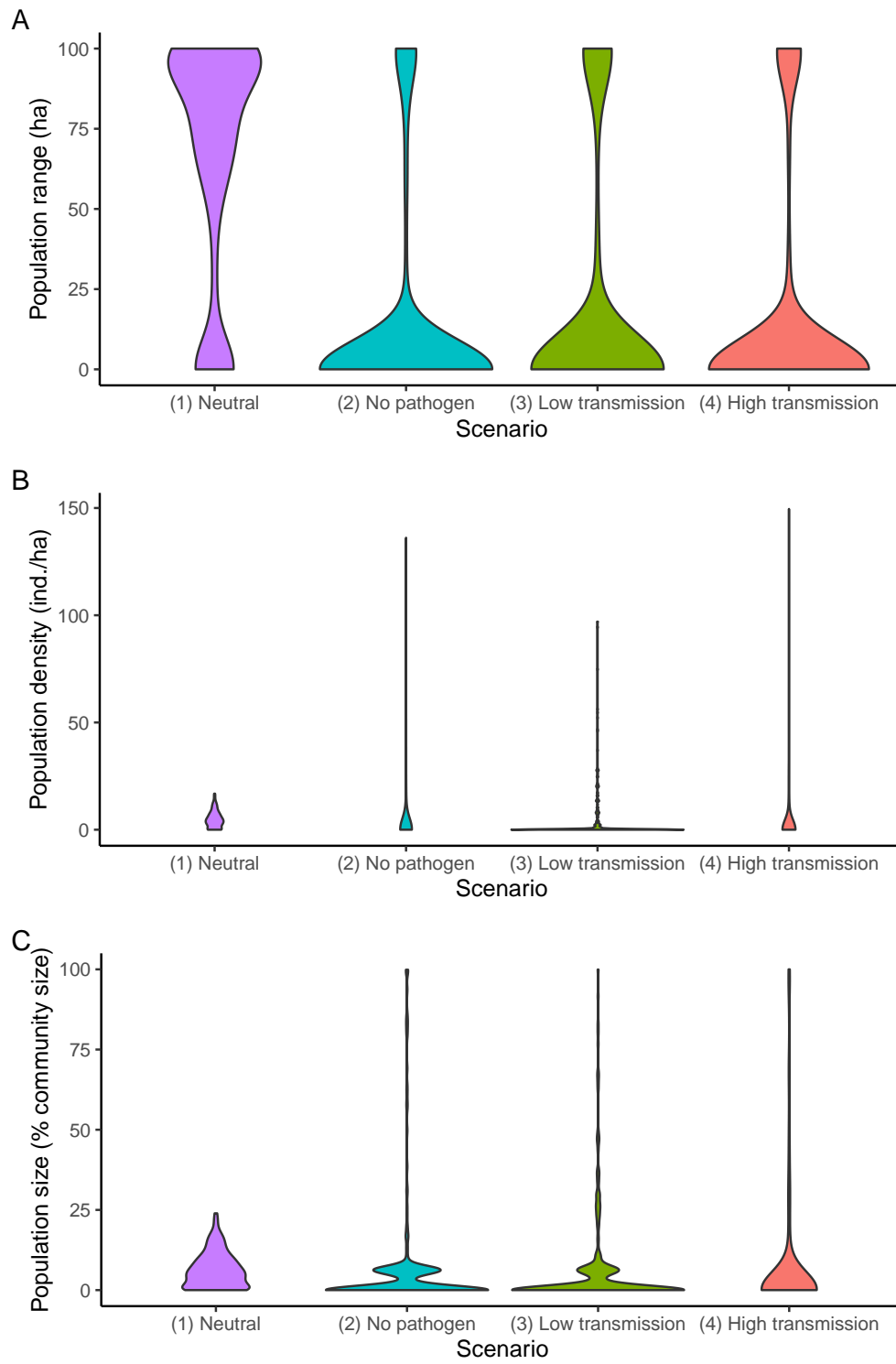


Figure 5: Range, density, and relative population size after 1000 updates, 320 data points per scenario (20 replicates with 16 species).

scenarios. For scenario 4 (high transmission), a Hubbell pattern was expected, i.e. a positive density- (and distance-) dependence of reproductive success. In line with this, it showed greater population densities and smaller range sizes than scenario 3.

## 4.2 Model caveats

Due to the constrained time frame of the modelling course, a few issues remain with the model which, under normal circumstances, would have been fixed prior to the publication of results. Three issues in particular ought to be mentioned.

First, there was a bug in the initialisation routine, which sometimes caused a small number of trees (generally less than five) to disappear before the start of the first update. This turned out to be a particularly difficult bug to track, as its appearance and effect seems to be contingent upon the traits and sequence of the trees as initialised by the random number generator.

The second bug was caused by an integer overflow in the dispersal routine, which caused the software to crash in about one in twenty runs. (Again, this was affected by the RNG.) As with the previous bug, a tight schedule did not allow me to find the root cause of the problem. However, both bugs should not affect the core validity of the model, their primary effect being to reduce the effective sample size.

The third and last issue was my implementation of the trees' dispersal kernel. In agreement with my supervisor, I chose to simplify the usual quasi-exponential distribution of seed dispersal into a uniform distribution, as this was significantly easier to implement. This may have increased the probability of finding a Janzen-Connell effect, as the  $I$  curve remained at a constant height instead of tapering off, thus increasing the total population recruitment (fig. 1). In future, an empirically tested dispersal kernel should be used, such as those described in Bullock et al. (2017).

## 4.3 Open questions

Beyond these technical issues, a range of biological questions await further exploration. These particularly concern the choice of default values for the various parameters of the model.

The overpowering effect of competitive exclusion may have been caused by the rather large mutation factor (50 %). If this were smaller, fitness differences between species would not be as pronounced, slowing down the rate of species loss over the runtime of the model, and reducing the difference between neutral and non-neutral scenarios.

The results of changes in the lethality of the pathogen are hard to predict, and ought to be tested. Raising it may reinforce a Janzen-Connell pattern and increase diversity; but could also increase species extinctions, thus having a net negative effect.

Finally, Hubbell and McCanny recruitment patterns are currently not distinguishable with the existing scenarios and the gathered data. To further test the predictions of Nathan and Casagrandi (2004), this would be a desirable extension of the model and its analysis.



## 4.4 Conclusion

In summary, the strongest influence on diversity at the end of the simulations was the presence or absence of interspecific competition. Nonetheless, there were detectable Janzen-Connell and Hubbell recruitment patterns in the scenarios for which they were predicted. Both were weak, but a different choice of parameter values may make them more conspicuous in future experiments. These results serve to confirm the generality of previous empirical and theoretical studies on the topic, while highlighting the difficulty of making quantitative predictions in complex ecological systems.

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