INVERTEBRATE SUCCESSION WITHIN THE FRUIT OF TAHITIAN CHESTNUT *Inocarpus fagifer* IN MOOREA, FRENCH POLYNESIA

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Abstract: The process of succession takes place over a broad range of magnitudes and timescales. Studies of animal succession within short-lived microhabitats are few in number, making it an important addition to the ecological literature. The decomposing fruit of the Tahitian Chestnut tree *I. fagifer* represents such a microhabitat. In this study, chestnut fruits from the island of Moorea, French Polynesia, were collected at different stages of decomposition, and the invertebrates inside were catalogued and identified to the most specific taxonomic category possible. Pitfall traps were set up at each location where chestnuts were collected in order to ensure that the dynamics of the chestnut habitat were different than the dynamics of the forest floor. Species richness and diversity for the chestnuts and pitfall traps were calculated and compared in order to test for trends of succession. There were no significant differences in richness or diversity for the pitfall traps, but significant differences did occur across stages for the chestnuts. Predictable trends of succession were interpreted from these results, suggesting that some form of facilitative succession was taking place.

INTRODUCTION

The process of succession is the orderly and predictable change of species composition and structure within ecological communities through time (Pickett and Collins 1987). It takes place in habitats that have either been recently disturbed, or previously unoccupied, since this leaves open ecological niches for new species colonization(Connell and Slatyer 1977). As the species change, so do the characteristics of the habitat since different species interact with the environment in different ways. The habitat change influences colonization by new species whose preferences are met by the newly created conditions. This process of continuous species replacement occurs across a broad range of timescales and habitat types. Practically any newly created or heavily disturbed habitat will undergo some form of succession, making the process an important focus of ecological study (Bazzaz 1979).

Researchers typically distinguish between primary and secondary succession. Primary succession refers to the predictable change in community composition after a new habitat has formed (Chapin 1994). The formation of new habitats is constantly occurring at different scales, such as retreating glaciers that leave large areas of exposed land, or a leaf that has recently fallen to the ground. These examples, while extremes in magnitude, both act as blank canvasses for the colonization of new species, and therefore are starting points for primary succession. Secondary succession refers to the predictable change of community composition in a habitat that has been disturbed, perhaps by natural causes like a fire or flood, or human-induced causes like forest clearing. In this case the habitat already existed, but the disturbance opened up niches for the colonization of new species (Guevara 1986). There have been a number of pathways or mechanisms through which the sequences of succession have been observed to take place (Connell and Slatyer 1977). One of the most common mechanisms, although there are many more, is referred to as facilitative succession, where a colonizing species affects the habitat in such a way making it more suitable for future successional species to thrive (Chapin 1994).

Some of the earliest studies of succession within insect communities focused on primary succession, and how insect communities changed within the habitat of decomposing carcasses (Bornemisszа 1957). Today, decomposition is still a major focus for the field of forensic entomology which uses the predictable sequence of insect colonization on corpses to determine the time of death in criminal investigations (Andersen 2001). Many things in nature, such as fallen fruit from a tree, are potential candidates with which to study primary succession of invertebrate communities, but outside of forensic entomology, relatively little research has been done.

On the island of Moorea in French Polynesia, I observed the Tahitian Chestnut tree *Inocarpus fagifer* (Hammes and Putoa 1986) bears a fruit that when fallen, becomes infested with a number of insects and invertebrates throughout its decomposition. This decomposing fruit acts as a microhabitat which changes radically over a relatively short timescale. Studying such a habitat provides insight into a changing community structure with a large number of potential replicates. This allows for a comparison of species richness and diversity at different stages of decomposition in order to see what kind of trends of invertebrate succession are taking place.

I proposed that some form of succession was occurring within the decomposing fruit of *I. fagifer*. To test this hypothesis I developed a study where a large number of *I. fagifer* fruit samples were collected at different stages of decomposition, and the invertebrate communities within them were catalogued and identified. The species richness and diversity between stages were then compared to test for trends of succession within the timescale of the fruits' decomposition and see if specific successional pathways could be observed.

MATERIALS AND METHODS

Site description

Eight separate plots were chosen on Moorea at mid-elevations (200-250m) between the upper Oponuhu and Pao Pao Valleys (Figure 1).These eight plots were all in one general area in order to minimize factors that could alter species composition such as elevation, precipitation, etc. Each plot consisted of a ten meter radius circle in an area of dense *I. fagifer* forest, where the canopy cover varied from about 85-90%.

FIG 1. Map of Site

Classification of decomposition stages and assessment of classification accuracy

Based on field observations between the eight sites, I developed a classification key identifying six stages of *I. fagifer* fruit decomposition. Eight freshly fallen chestnuts were collected from within my site and monitored once a week for six weeks to determine whether the classification system correctly identified the progression of decomposition. The timescale of decomposition was also assessed through this monitoring.

Chestnut collection and invertebrate identification

I selected chestnuts within my plots by randomly generating six azimuths and picking the first chestnut that corresponded to each of my six decomposition groups. I set up a pitfall trap at every collection point in order to compare invertebrates found around the fruit, and those found on or within it. The pitfall traps were 6 cm diameter plastic cups filled with a soapy water solution, and buried so the edge of the cup was flush with the ground. They were collected after two days and their contents were catalogued and identified in the lab.

Once the study chestnuts were collected, each sample was frozen separately in order to immobilize the invertebrates that may have easily escaped. After freezing, a census was carefully performed on each sample, cataloguing the invertebrates found inside. The invertebrates were identified to different extents. Many were identified to family, some were identified more specifically, and some were qualitatively described as different morphospecies. A microscope picture was taken of each new invertebrate observed so there would be an accessible record of what was found. Specimens were also taken and packaged in an ethanol preservative. All voucher specimens will be deposited in the Essig Museum of Entomology at the University of California, Berkeley.

Analysis of data

Once the data were collected, functional roles were assigned to a subset of the invertebrates found, and their changes through time were observed. I calculated a value for species richness (S), as well as a Shannon diversity index (H`) averaged over each stage for the eight plots. I compared the biological diversity index, which measures species evenness, with values for species richness. This is a common step in analysis of successional studies (Whittaker 1994). I used Jump Version 5.1 (SAS Institute Inc.) to visualize a plot of the mean species richness and diversity indexes against the six stages of decomposition. A Tukey-Kramer HSD test was performed on these plots to see if there were statistically significant differences between the community compositions at different stages. I analyzed the results to see if trends of succession could be observed.

In order to compare the invertebrates collected within the chestnuts, and those collected in the pitfall traps, I also calculated a mean value for species richness and diversity for the pitfall trap communities averaged over each stage. The pitfall results were compared with the chestnut results to see if changes in chestnut species richness and diversity were significantly different than the background richness and diversity of the forest floor.

RESULTS

Classification of decomposition stages

Based on field observations, I developed a timeline consisting of six stages to characterize the decomposition of the *I. fagifer* fruit (Figure 2). This timeline represents three possible routes of decomposition; the fruit decomposes relatively undisturbed, the fruit begins to decompose undisturbed until it germinates, or the fruit is cracked open by a

Timeline of Decomposition

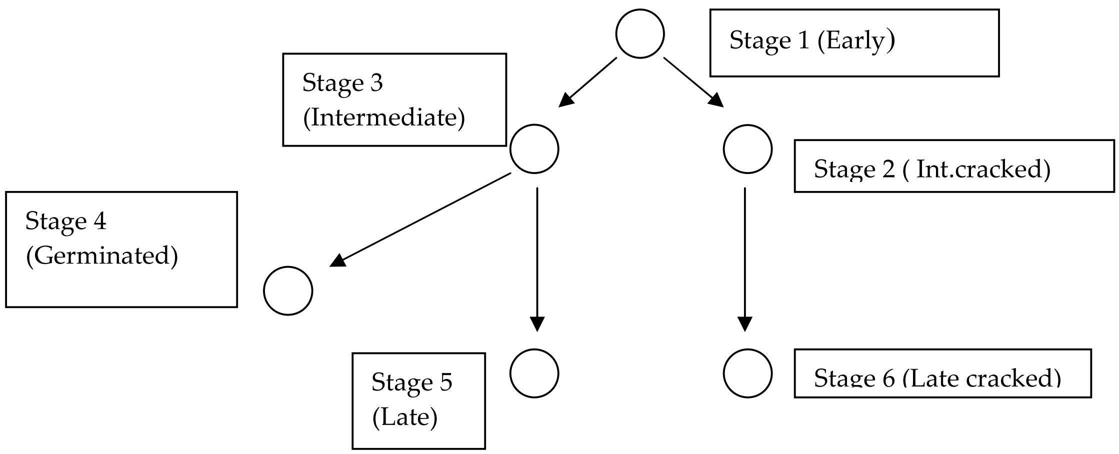

FIG 2. Stage 1 represents a freshly fallen fruit with hard outer skin. Stages 2 and 3 represent an intermediate decomposition with a mixture of hard skin and fibrous husk. Stage 4 represents a chestnut that has germinated. Stage 5 and 6 represent a late stage of decomposition where the chestnuts are completely brown and fibrous

rat or bird leaving it prematurely exposed to the forest floor.

The fruits which most recently fell from the trees were characterized by a hard and glossy green and yellow skin surrounding a thick husk that protected the endosperm in the center. They would go on to an intermediate stage of decomposition where their outer skin would retain the original characteristics in some parts, while in other places the hard outer skin was gone, leaving the brown soft husk exposed. This stage was also observed with the fruits that were cracked open, but they were counted as separate parallel stages since the two habitats were so different. The final stage of decomposition was characterized by only the fibrous brown husk being present, and this too was the final stage for cracked fruits. The one other stage I defined was when the seed germinated, which appeared to take place sometime after the intermediate decomposition since they always had the fibrous brown husk.

Assessment of classification accuracy

The eight freshly fallen chestnuts were monitored for six weeks and all decomposed at roughly the same rate. There were some fluctuations in appearance from week to week, but by the end they all looked the same. The hard outer skin was still present on all of them, but it was brown and no longer hard. The fibrous husk was also visible in parts, indicating that after six weeks these fruits were all in a stage of late intermediate decomposition. This experiment suggests that the timescale of decomposition is much higher than six weeks since none of the fruits reached the final stage of decomposition.

Species composition and trends through time

A total of forty six morphospecies were observed from all the chestnuts collected. Of these forty six morphospecies,

TABLE 1. Taxonomic groups, number of morphospecies and hypothesized functional groups from collected chestnuts across decomposition stages.

Name	Number of morphospecies	Predicted Functional Group
Staphylinidae spp. (Rove Beetle)	3	Predator
Acarina (Mite)	3	Herbivore
Dipluran spp.	1	Herbivore
Small Orange Beetle	1	Herbivore
Small Larva	1	Herbivore
Tineidae Larvae	1	Herbivore
Scotlytidae spp.	1	Herbivore
Pheidole (Ant)	2	Forest Floor
Amphipod	1	Forest Floor
Microgastropod	3	Forest Floor
Centipede	1	Forest Floor
Millipede	3	Forest Floor
Cryptophlebia pallifimbriana	1	Herbivorous Colonizer

twenty two were placed in to functional groups for further analysis (Table 1). The remainder of the individuals were either found so infrequently as to be considered insignificant, or functional groups could not be determined. The functional groups included herbivores, predators, herbivorous colonizers and forest floor individuals. The herbivorous colonizers group refers to one species (*Cryptophlebia pallifimbriana)* that appears to play a major role in the system and will be further discussed in detail. The forest floor individuals refer to the morphospecies found in the chestnuts that overlap with morphospecies predominantly found in the pitfall traps. A graph was generated to show how these functional groups proportionally varied on average across stages (Figure 3). This was done by calculating what percent of the community the individuals in each functional group represented and then averaging across the eight plots.

The early stages of the fruits' decomposition were dominated by a colonization of the larvae of the moth *Cryptophlebia pallifimbriana* (Hammes and Putoa 1986*)*. This species is described by the group of herbivorous colonizers and in the first stage they represented, on average, about fifty percent of the individuals found. These larvae would bore into the inner fruit at a very early stage, possibly even while the fruit was still on the tree. It was observed that in later stages the tunnels of these larvae were still noticeable, long after their departure from the microhabitat of the fruit. The possible role of these larvae will be discussed in detail later.The non-cracked intermediate stage did not exhibit any prominent trends, other than

TABLE 2. Mean Abundance of Individuals Across Stages

Stage	Mean Individual Abundance
Early	28
Intermediate Cracked	40
Intermediate	19
Germinated	3
Late	52
Late Cracked	10

Note: There was one plot where over 100 individuals of ants were found in the early stage, resulting in a major outlier and a high average number.

the proportional reduction of *C. pallifimbriana* by about half. None of the cracked open chestnuts at this stage were found to have *C. pallifimbriana*. They also had a surprisingly low proportion of forest floor individuals considering they were so exposed to that habitat

The germinated seeds had the lowest average number of individuals of all the stages (Table 2). For these chestnuts the endosperm was always completely intact, with no signs of previous tunnels by *C.pallifimbriana*.

The later stages of decomposition were characterized by large numbers of mites, small orange beetles and other small herbivores. These orange beetles were often very great in number and appeared to feed on the decomposing husk and frass. Millipedes were frequently observed, as well as smaller larvae from the family Tineidae. The cracked chestnuts in this stage were similar, but had smaller proportions of herbivores and a much higher proportion of forest floor individuals such as microgastropods, millipedes and ants.

Species richness and diversity were calculated for each stage and averaged over the eight plots for both the chestnuts and pitfall traps (Figures 4a-4b). The pitfall trap results showed no significant difference between stages for species richness (p=0.92) or species diversity (p=0.98). The chestnuts did have significant differences between stages for species richness (p=0.0001) and species diversity (p=0.0009). The general trends between the two measurements were very similar. The first stage and germinated stage had the lowest species richness (S_{early} = 1.75 and S_{germ} = 2) and lowest diversity ($H`_{early}$ = 0.40 and $H`_{germ}$= 0.49). The two cracked stages had the highest diversity ($H`_{int\ cracked}$ = 1.20 and $H`_{late\ cracked}$ = 1.25), followed closely by the last stage of decomposition ($H`_{late}$ = 1.11). These three stages also had the highest species richness ($S_{int\ cracked}$ = 5.00, $S_{late\ cracked}$ = 4.38, and S_{late}= 5.75).

DISCUSSION

The *I. fagifer* fruit is a unique habitat to study for successional dynamics because it is a relatively closed system with its hard outer skin, as compared to a more exposed habitat like a fallen leaf or decomposing body. The *C. pallifimbriana* larvae are the first macro-

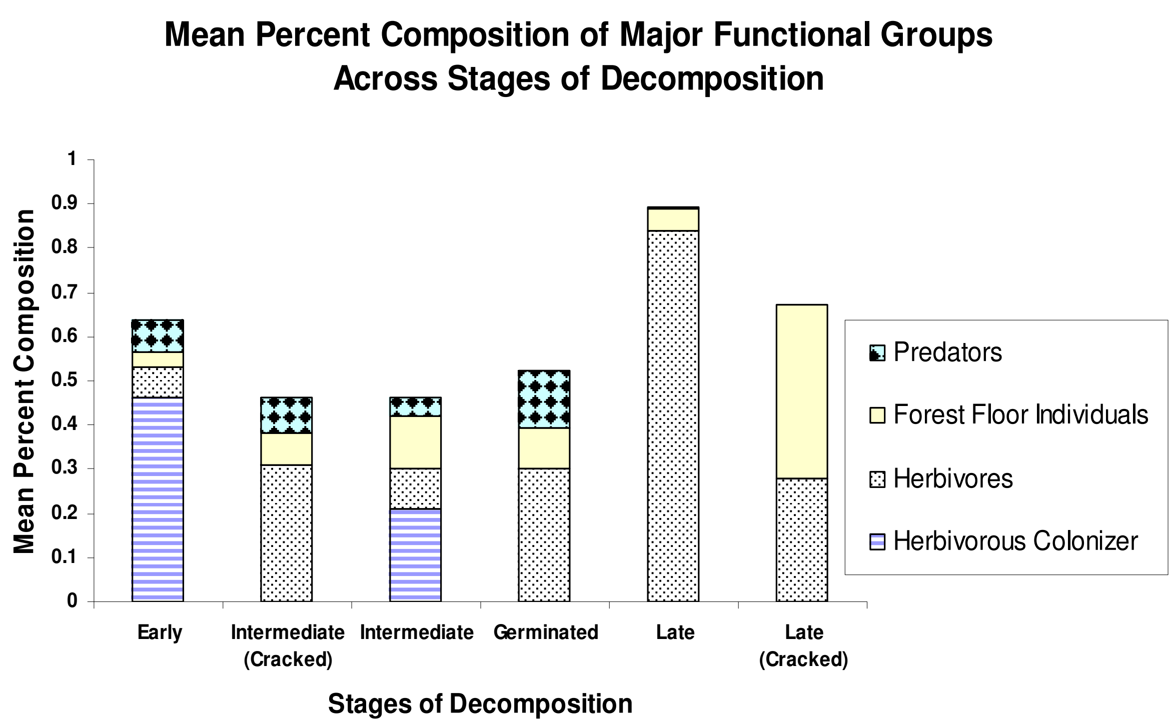

FIG 3. Shows average percent composition of the difference functional groups through time. The herbivorous colonizer is the species *Cryptophlebia pallifimbriana.* Note the numbers do not add to one hundreded because these represent only the major functional groups.

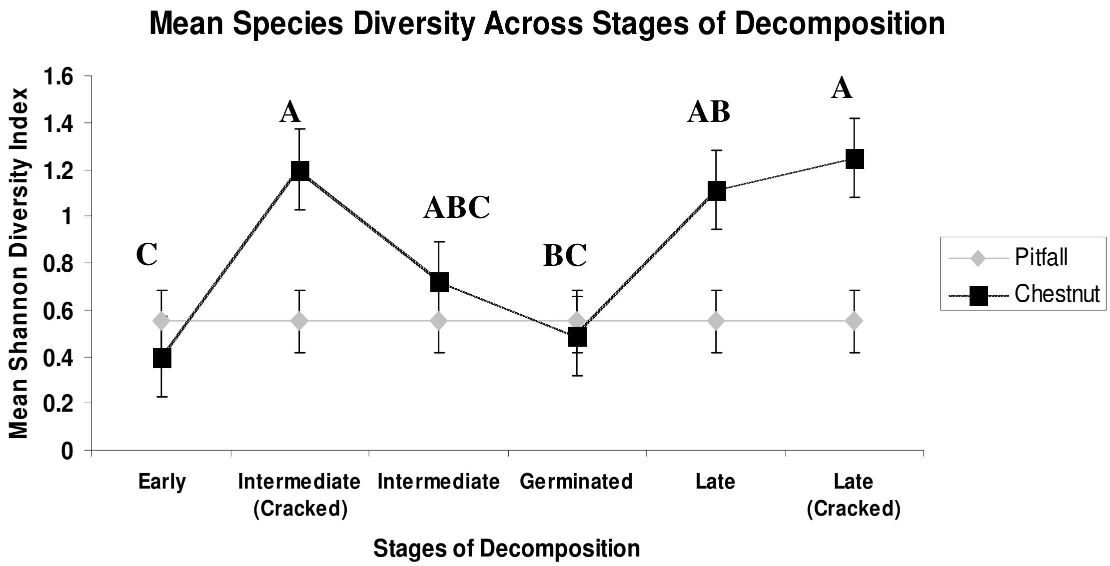

FIG 4a. Because the Tukey test showed no significant differences between stages for the pitfall traps, and they are meant to show general background richness, an average line was generated. Different letters reflect significant differences between stages for chestnut results (p = 0.0009).

organisms to bore into the fruit and by doing this they make the interior accessible to all future species. The data suggest that these larvae are the crucial colonizing species in a facilitative succession within the fruit.

The first stage had the lowest diversity, which is characteristic of diversity in early succession since the habitat is only suitable for the colonizing species at that early time. In this case it is dominated by *C. pallifimbriana* which makes the habitat accessible, digests the fruit, and leaves frass for small insects to feed on. Further evidence for facilitative succession is given by two of the early stage chestnuts I collected that had nothing found inside. The larvae were not present, and neither was any trace that they had been present, so nothing was able to access the habitat.

Results from the germinated chestnuts also support this interpretation. Based on the condition on the outside of the germinated fruits, which resembled the characteristics of

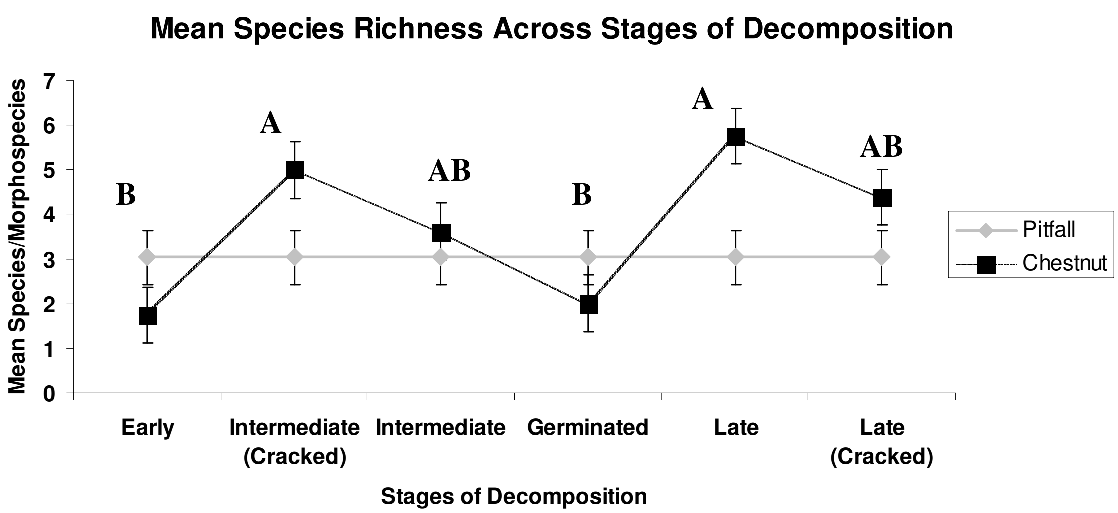

FIG 4a. As in previous figure, pitfall results showed no significant difference so an average line was generated. Different letters reflect significant differences between stages (p = 0.0001).

late decomposition, these fruits have been on the forest floor for a long time. The late stage of decomposition was characterized by high diversity and large numbers of small herbivores, and it could be expected that a chestnut that has been on the forest floor for a similar period of time would exhibit the same trends. However, the mean diversity of this stage was almost as low as the first stage and consistently had the lowest number of individuals compared to other stages (see Figures 3 and 4 and Table 2). When the chestnuts were cut open, the endosperm was completely intact, indicating that colonization by *C. pallifimbriana* never occurred. This could suggest that the larvae represent some limiting factor for *I. fagifer* seed germination. The absence of caterpillars ensures the absence of future species, allowing the endosperm to remain intact and able to germinate.

Further manipulative experiments could be performed to strengthen these interpretations. It would be useful to know if the caterpillars do anything other than allow access to the fruit to make it more suitable for future species, such as making the endosperm more digestible, or leaving frass. Germination experiments could also be conducted to see to what extent the absence of caterpillars promotes germination.

The pitfall traps were set up as a control to test that there were changes in species composition within the fruit, independent of the background species composition of the forest floor. My data confirm this as seen by comparing the graphs of the two mean indexes. In the non-cracked samples there were very few species that were found in both the chestnuts and the pitfall traps. Ten morphospecies out of a total forty six were found to overlap with morphospecies collected in the pitfall traps, suggesting that the organisms inside the fruits are not moving in high frequencies from fruit to fruit.

Succession refers to a predictable and orderly change in species composition through time. As previously discussed, the early trends were predictable. The late trends were also predictable as herbivores came to dominate the habitat. The intermediate decomposition stages were less predictable because there did not seem to be any species that dominated the system across all eight plots. This could be because the habitat was going through a transition as the colonizing larvae leave and all of a sudden the system is open to a large number of species. The cracked chestnuts had the highest diversity because they contained the species of two habitats; the interior of the fruit and the forest floor. Not counting the cracked or germinated stages, there is an almost linear increase in diversity through decomposition. It would be beneficial to create a more stringent classification for decomposition to get a clearer picture of how the communities change. Little additional information could be taken from my experiment to assess the accuracy of my classification system. The results showed that the timescale of decomposition is longer than six weeks, but any guess of how long it would take is pure speculation.

Trends of succession were observed in the fruits, but many more tests and experiments could be done to strengthen the hypothesis. Functional roles within a family can be highly variable, and the groups I placed certain species in were by no means definitive. A more complete description of functional groups within the chestnut would be advantageous for further study of succession since many species may differ, but their roles within the habitat stay the same. Despite these limitations, there does appear to be some form of predictable species replacement taking place, as well as patterns that resemble facilitative pathways, suggesting that my hypothesis should not be rejected.

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