



The dynamics of strangling among forest trees



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HIGHLIGHTS

- Strangler trees germinate atop other trees, potentially replacing their host trees.
- Hemiepiphytic strangler trees exploit high-light availability in tree crowns.
- We use evolutionary game theory to model the conditions for strangling to evolve.
- Threshold germination rates for strangling to be evolutionarily stable are derived.
- We assess the evolutionary stability of commensalism between hemiepiphytes and hosts.

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ABSTRACT

Strangler trees germinate and grow on other trees, eventually enveloping and potentially even girdling their hosts. This allows them to mitigate fitness costs otherwise incurred by germinating and competing with other trees on the forest floor, as well as minimize risks associated with host tree-fall. If stranglers can themselves host other strangler trees, they may not even seem to need non-stranglers to persist. Yet despite their high fitness potential, strangler trees neither dominate the communities in which they occur nor is the strategy particularly common outside of figs (genus *Ficus*). Here we analyze how dynamic interactions between strangling and non-strangling trees can shape the adaptive landscape for strangling mutants and mutant trees that have lost the ability to strangle. We find a threshold which strangler germination rates must exceed for selection to favor the evolution of strangling, regardless of how effectively hemiepiphytic stranglers may subsequently replace their hosts. This condition describes the magnitude of the phenotypic displacement in the ability to germinate on other trees necessary for invasion by a mutant tree that could potentially strangle its host following establishment as an epiphyte. We show how the relative abilities of strangling and non-strangling trees to occupy empty sites can govern whether strangling is an evolutionarily stable strategy, and obtain the conditions for strangler coexistence with non-stranglers. We then elucidate when the evolution of strangling can disrupt stable coexistence between commensal epiphytic ancestors and their non-strangling host trees. This allows us to highlight parallels between the invasion fitness of strangler trees arising from commensalist ancestors, and cases where strangling can arise in concert with the evolution of hemiepiphytism among free-standing ancestors. Finally, we discuss how our results can inform the evolutionary ecology of antagonistic interactions more generally.

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1. Introduction

A major goal in evolutionary biology and ecology is to understand how inter-specific interactions drive adaptation, and elucidate how such adaptations, in turn, govern community structure. Competition between individuals for access to resources can substantially reduce the fitness of many organisms (e.g., Gause, 1934), and selection to improve competitive performance or otherwise mitigate

competition's detrimental fitness effects can drive the evolution of morphological structures as well as select for novel behavioral and life history strategies (e.g., Darwin, 1859; Abrams, 1990, 1999; Zobel, 1992; Blossey and Nötzold, 1995; Schluter, 2000; Dayan and Simberloff, 2005; Stuart and Losos, 2013). For several plant species, competition over access to space, light, mutualists and below-ground nutrients as well as other resources can be intense (e.g., Grace and Tilman, 1990; Goldberg and Barton, 1992; Wright, 2002; Brooker et al., 2008), and many plants have evolved adaptations to improve competitive performance or mitigate detrimental competitive effects (e.g., Grime, 1977; Taper and Case, 1992; Blossey and

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Nötzold, 1995; Feng et al., 2009). Such adaptations in organismal traits can, in turn, govern the trajectory of ecological dynamics by modifying parameters affecting interaction strengths between species, thereby creating a feedback between adaptive change and the structure and composition of plant communities (reviewed in, e.g., Hairston et al., 2005; Post and Palkovacs, 2009; Vasseur et al., 2011; Lankau, 2011; Strauss, 2014).

One relatively less studied adaptation for evading competitive pressure in plants is strangling (e.g., Dobzhansky and Pires, 1954; Lawton, 1986; Hao et al., 2013). The seeds of strangler trees, most famously of the genus *Ficus*, are deposited in crevices of older, mature trees where they germinate (e.g., Putz and Holbrook, 1986; Benzing, 1990; Zotz, 2013). Beginning their lives as epiphytes, strangler trees grow not only upward to maximize light intake, but also expand their roots downward to envelop their hosts (e.g., Lawton, 1986; Daniels and Lawton, 1991). By growing atop their hosts, the foliage of strangler trees can potentially shade their hosts' foliage, depriving the host trees of light. Moreover, once strangler roots reach the forest floor, because of their close spatial proximity to their hosts' roots, newly established stranglers may interfere with their host tree's ability to acquire essential soil nutrients. They may also girdle and ultimately kill their hosts (Ramírez-Benavides, 1977; for some exceptions, see Putz and Holbrook, 1989). By germinating on other trees, strangler trees can mitigate fitness costs they may otherwise incur if they had to germinate and compete with neighboring trees on the forest floor (e.g., Hao et al., 2013), particularly when light (or germination sites with sufficient light) is a prominent limiting resource (as it can be in many tropical forests – e.g. Poorter, 1999; Kraft and Ackerly, 2010). Moreover, stranglers which establish as free-standing trees may escape mortality risks associated with host tree-fall, a potential source of mortality for plants germinating in tree crowns that do not strangle (Harrison et al., 2003; Harrison, 2006). Finally, if stranglers ultimately displace their hosts, they may preempt the offspring of other trees from germinating nearby. This can lead to a competitive asymmetry vis-à-vis non-strangling trees: mature stranglers can shade and block non-strangling seedlings growing on the forest floor, but mature non-stranglers may be less effective at depriving stranglers of light. By contrast, if stranglers can germinate atop their non-strangler hosts, their ability to acquire light may be considerable as they are no longer as heavily shaded as they would have been had they germinated on the forest floor like their non-strangling competitors.

Hemiepiphytism – the ability of structurally dependent plants that begin their lives as epiphytes to subsequently develop aerial roots to establish on the forest floor (e.g., Zotz, 2013) – appears to have evolved independently on at least four occasions within *Ficus* (Hao et al., 2013), although not all figs germinating on other trees strangle their hosts (e.g., Benzing, 1990; Harrison et al., 2003; Harrison, 2006). While all stranglers exhibit a hemiepiphytic life stage, not all hemiepiphytes are necessarily stranglers. Thus, hemiepiphytism may evolutionarily precede strangling, with non-strangling hemiepiphytes representing the ancestral state. Such non-strangling hemiepiphytes may have a largely commensalist interaction with their hosts (i.e., the hemiepiphytes benefit from their host tree but do not adversely affect the host's fitness). However, some traits, particularly for *Ficus* trees, may render them uniquely preadapted to strangling. For instance, Ramírez-Benavides (1977) noted how figs have their seeds dispersed by flying frugivores, and are effective at conserving water following germination. If such trees tend to also rapidly produce robust aerial roots, strangling may be a necessary by-product that may have co-evolved with the ability of some figs to germinate on their hosts (Ramírez-Benavides, 1977).

Yet despite their high fitness potential and even possible competitive advantage, strangler trees do not dominate the communities in which they are found, and the strategy is rare outside of *Ficus*. Several proximate mechanisms restricting strangler abundance have been proposed. For instance, Swagel et al. (1997) illustrate how the strangler

tree *Ficus aurea* requires high water potential in the substrate to germinate – substrates which, in the Bahamian dry forests they studied, restricted them to germinating in palm leaf bases. Yet even in wet evergreen forests, stranglers are rarely the dominant species (e.g., Corner, 1952; Kochummen et al., 1990; Nadkarni et al., 1995; Condit et al., 1999, 2012; Theilade et al., 2011). Host microenvironments may provide alternative limitations on strangler establishment (Putz and Holbrook, 1986, 1989; Laman, 1995; Athreya, 1999; Harrison et al., 2003); seed disperser behavior, host bark texture and structure can also potentially constrain strangler fitness (Guy, 1977; Todzia, 1986; Patel, 1996).

Thus, while proximate constraints may help explain how the fitness advantages of strangling can be reduced, they may not answer the question of why strangling is not more common. Given the potential fitness benefits of a strangling life history strategy, it may seem paradoxical that so few trees strangle. Resolving this question requires elucidating the conditions under which a strangling life history strategy can have higher fitness consequences than a non-strangling life history strategy. Because of the nonlinearities inherent in the competitive and evolutionary dynamics of strangler-host tree interactions, mathematical analyses can clarify constraints governing whether strangling can evolve among trees.

Here we model the conditions favoring the evolution of strangler trees from non-strangling ancestral populations, where the evolution of strangling is intimately linked to the evolution of hemiepiphytism. We analyze and compare how different inter- and intra-specific mechanisms drive the population and evolutionary dynamics of strangler trees. Finally, we analyze the conditions under which a hemiepiphytic ancestor may cease to have commensal interactions with their hosts trees and evolve strangling. These analyses are key to elucidating the conditions that facilitate or impede the ability of stranglers and non-stranglers to coexist.

2. Model description

The model characterizes the dynamics of a mutant strangler lineage invading a resident forest community consisting of non-strangler trees. The model is formulated to describe a forest in which individual trees occupy discrete patches. The total number of patches, k , is assumed to be constant. A given patch's state can vary over time, and we model a forest where each patch can be categorized into one of the following states: (i) empty patches, (ii) patches occupied by a non-strangling tree that is not hosting a strangler, (iii) patches occupied by a non-strangling host and an epiphytic strangler, (iv) patches occupied by stranglers, and (v) patches occupied by stranglers hosting other epiphytic stranglers. As the total number of patches is constant, the number of empty patches at a given point in time is simply k subtracted by the sum of the non-empty patches.

We assume that each patch can only be occupied by a single mature tree, although mature trees may also act as hosts for epiphytes as well. Non-strangling host trees can establish in empty patches (i.e., colonize understory gaps with sufficient luminescence) at a rate $m(N_n + N_{ns})$, where N_n is the number of non-strangling trees in the forest that occupy a patch alone and are not hosting stranglers, and N_{ns} is the number of non-strangling trees hosting stranglers and thus occupy a patch with a strangler epiphyte. The per-capita establishment rate m is the product of the number of seeds or propagules produced per tree, the fraction of those propagules that successfully germinate in the gap, and the rate at which germinating seedlings are recruited into the adult host tree population. For both stranglers and non-stranglers, we assume an island model of dispersal (e.g., Wright, 1931), which might be reasonable if, for instance, seed dispersal occurs via wind or avian frugivores (as is common in strangler figs – e.g., Ramírez-Benavides, 1977). This assumption results in a well-mixed

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