

## Evolution of transmission mode in obligate symbionts

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### ABSTRACT

**Background:** A host obtains symbionts by horizontal transmission when infected from the environment or contagiously from other hosts in the same generation. In contrast, vertical transmission occurs when a host obtains its symbionts directly from its parents. Either vertical or horizontal transmission can sustain an association between a host and its symbiont.

**Questions:** What evolutionary forces are necessary to evolve from an ancestral state of horizontal transmission to a derived state of vertical transmission?

**Mathematical methods:** We explore a general model of fitness interaction, including both additive and epistatic effects, between host and symbiont genes. Recursion equations allow us to analyse the short-term behaviour of the model and to study long-term deterministic effects with numerical iterations.

**Key assumptions:** Obligate interaction between a symbiont and a single host species with genetically determined horizontal and vertical transmission. No free-living symbionts or uninfected hosts and each host is infected by only a single symbiont genetic lineage (no multiple infections). No population structure.

**Conclusions:** Epistasis for fitness between host and symbiont genes, like that in a matching alleles model, is a necessary condition for the evolution of vertical from horizontal transmission. Stochastic individual-based simulations show that (1) mutation facilitates the switch to vertical transmission and (2) vertical transmission is a stable evolutionary endpoint for a matching alleles model.

*Keywords:* co-evolution, epistasis, horizontal transmission, linkage disequilibrium, vertical transmission.

### INTRODUCTION

Intimate host–symbiont associations are ubiquitous in natural communities (Bright and Bulgheresi, 2010; Toft and Andersson, 2010). Many exhibit life-history adaptations to ensure horizontal or vertical transmission, and some hosts employ both modes of symbiont acquisition (Bright and Bulgheresi, 2010; Sachs *et al.*, 2011). For instance, most plant species are known to form symbiotic associations with mycorrhizal fungi that colonize roots (Rodriguez *et al.*, 2009). Many legumes

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