When 'isms collide: mutualisms, commensalisms, and antagonisms among plant enemies.

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Postulates of a tentative new theory regarding plant pestilence

P1: Symbioses are common among plant enemies

P2: Symbioses tend to be mutualisms and commensalisms

P3: Plant pestilence is usually the result of extreme population fluctuations in plant enemies

P4: Population fluctuations are wrought by complex endogenous dynamics and/or variable exogenous effects

Postulate 5: Commensalisms, and especially mutualisms, tend to destabilize population dynamics

- P5a: increased variance in per capita growth rates (R_t) from exogenous effects
- P5b: increased variance in R_t from complex endogenous dynamics.

$$R_t = \underbrace{f(N_t, N_{t-1} \ldots N_{t-f})}_{\text{P5a}} + \underbrace{\sigma_{\text{exogenous}}}_{\text{P5b}} + \sigma_{\text{demographic}}$$

P5a: Symbioses promote nonlinearities & provide larger target for delayed feedbacks

P5b: Symbioses broaden the spectrum of exogenous demographic effects and amplify them

Tarsonemus mites +/+

Ophiostoma minus -/-

Mycangial fungi +/+

Dendroctonus frontalis +/-

Trees

P5a

Exogenous effects on population dynamics

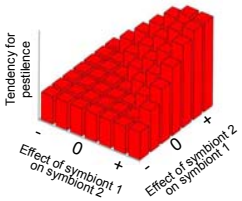
Birds +/-

Caterpillars +/-

Trees

Support for generality from:

1. Intrinsic mathematical instability of mutualisms (May 1982)
2. Control theory from engineering (Maxwell 1868): e.g., positive feedbacks in electrical circuits amplify noise



Logical outcome of P2-P6

= "*Pestis symbiotica*", a putative pattern and a tenative theory

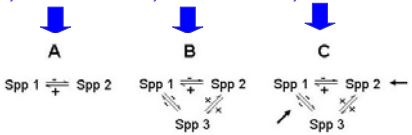
Plant pest quarantine list — Putative cases of *Pestis symbiotica*

Western Europe (EPPO)	214 spp	47%
United States (APHIS)	306 spp	45%

Interaction system normally invoked to explain complex endogenous dynamics

Mutualisms enrich the potential for density-dependent feedback systems that can include delays and nonlinearities

The larger the interaction system, the greater the potential for exogenous effects on population dynamics

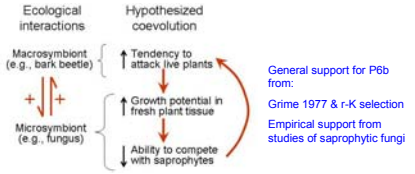


Three hypothetical interaction systems. Spp 1 is a predator or pathogen of Spp 2. Spp 2 and 3 are mutualists. Spp 1 and 3 are competitors. The heavy arrows in C represent exogenous climatic effects on Spp 2 and on the competitive interaction between Spp 1 and 3.

Postulate 6: Symbioses among plant enemies promote pestilence in evolutionary time

P6a: Symbioses that involve biotic vectors favor the evolutionary retention of virulence (Ewald 1994)

P6b: Symbioses among plant enemies can produce positive evolutionary feedbacks that amplify pestilence by promoting aggressiveness



General support for P6b from:

Grime 1977 & r-K selection

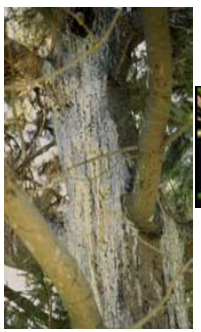
Empirical support from studies of saprophytic fungi

Coclusions given P1-P6…

- Many cases of plant pestilence are an emergent property of symbiotic associations among plant enemies (= *Pestis symbiotica*)
- Understanding and managing this class of plant pestilence involves understanding and managing the community interactions among plant enemies.

Other implications

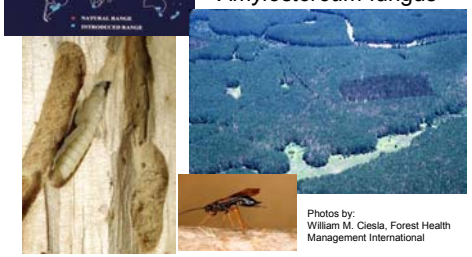
- May also be relevant to animal pestilence and human disease
- "Food web" theory requires expansion to accommodate positive interactions, which are generally not trophic interactions.
- *Pestis symbiotica* runs counter to a prevailing theme of symbiology: the emergence of cooperation among previously independent biological entities. Ironically, the theory predicts that symbionts as an ecological unit tend to become "red in tooth and claw".



Pitch canker
Fusarium fungus & spittlebugs

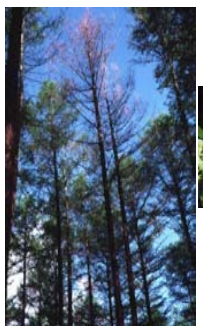
Pierce's Disease
Xylella bacterium & glassy winged sharpshooter

Pine wood wasp
Sirex wasp & *Amylostereum* fungus



Photos by:
William M. Ciesla, Forest Health Management International

Beech bark disease
Nectria fungus & two scale insects



Pinewood nematode
Bursaphelenchus & *Monochamus* beetles

Oak wilt
Ceratocystis fungus & nitidulid beetles

Dutch elm disease
Ophiostoma fungus, *Scolytus* beetles, (& *Tarsonemus* mites?)