



Commentary

Holt (1977) and apparent competition

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Volterra (1926) (see also **Volterra, 1928**) demonstrated that competition for a single, limiting resource regulates biodiversity by what now is known as the R^* rule: the competitor that suppresses the resource to the lowest equilibrium density excludes all other competitors. This empirically supported simple rule (**Wilson et al., 2007**) helped knight competition as a key determinant of community structure and initiated an ongoing quest to identify mechanisms permitting species coexistence.

Fifty years after Volterra's paper, **Holt (1977)** turned things upside down by studying non-competing prey species who share a common predator. For such communities, increasing the density of one prey species increases the common predator density, which exerts a negative effect on the other prey species and vice-versa. Thus, to the uninformed observer, the prey appear to be competing despite only interacting indirectly through the shared predator. Holt termed this novel mechanism apparent competition. With increasing levels of productivity, Holt demonstrated that prey species would be continually lost until only one was left standing: the prey species that can support the highest predator equilibrium density (P^*). Like its competitive counterpart, the R^* rule, empirical support for the P^* rule and, more generally, for apparent competition, has been mounting (**Chaneton and Bonsall, 2000; Holt and Bonsall, 2017**). Consequently, the implications of apparent competition for conservation biology are being seriously considered (**Gibson, 2006**).

Beyond introducing apparent competition, **Holt (1977)** is a cornucopia of ideas. Holt demonstrated the robustness of his conclusions (under equilibrium conditions) to including predator functional responses that account for predator saturation or predator switching behavior, and to alternative forms of prey dynamics. He also demonstrated that (i) including refuges from predation for one prey species can reverse the P^* -rule: the prey species supporting the lower density of predators leads to the exclusion of the other prey species, (ii) positive density-dependence in the prey growth rate can generate alternative stable states

supporting a single prey species, and (iii) switching or saturating predators can produce “short time periods...[of apparent] mutualism”, where increasing density of one prey species leads to a reduced predation rate on the other prey species. This short-term apparent mutualism can become long-term if the predator is regulated by a top predator. Following an extensive discussion of the potential role of trait evolution on apparent competition, **Holt (1977, pg. 23)** concluded “that if we are to develop a deep understanding of the relation between coevolution and community ecology, we must develop our evolutionary arguments in the context of explicit population dynamic models”. Although apparent competition is an indirect effect between two species mediated by one other species, **Holt (1977)** extensively discussed indirect effects in more complex foodwebs and suggested that “Levins' technique of ‘loop analysis’...may prove to be a useful tool for the elucidation of indirect interactions in complex communities”.

Four decades after its publication, it is remarkable how many of these ideas have blossomed in anticipated and unanticipated ways. Holt's suggestion about the utility of Levins' loop analysis was realized by **Bender et al. (1984)**, who developed methods related to Levins' loop analysis to identify all indirect effects of increasing one species equilibrium density on all other species' equilibrium densities in communities of arbitrary complexity. **Abrams et al. (1998)** showed that saturating predators could turn short-term apparent mutualism into long-term mutualism by destabilizing predator-prey interactions. New mechanisms for generating alternative stable states have been found, including prey simultaneously sharing a predator and a resource (**Holt et al., 1994**), predators exhibiting complex life cycles (**Schreiber and Rudolf, 2008**), and prey providing refuges to predators (**Orrock et al., 2010**). As suggested by **Holt (1977)**, the role of eco-evolutionary feedbacks on community dynamics by explicitly coupling evolutionary and ecological dynamics became and continues to be an area of active research (**Schoener, 2011**) with a significant presence in *Theoretical Population Biology* (see e.g., **Abrams, 1986; Matsuda and Abrams, 1994; Dieckmann and Metz, 2006; Mougi, 2012; Engen and Sæther, 2019**).

By highlighting a diversity of ways that mathematical thinking can inform biology, reading (**Holt, 1977**) played a pivotal role in

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transition of both of us from pure mathematicians to theoretical population biologists. Holt's statement that (Holt, 1977, pg. 215): "the above remarks apply to point equilibria; I do not know what happens when the system exhibits more complex behavior", motivated one of us to prove (Schreiber, 2004) that Holt's conditions for equilibrium coexistence also guarantee permanence (i.e. all species densities remaining bounded away from extinction for all positive initial conditions (Jansen and Sigmund, 1998)) when predator saturation generates oscillatory dynamics, while also showing that oscillatory coexistence without any coexistence equilibrium is possible. Furthermore, Holt's comments on eco-evolutionary feedbacks inspired us to study the effects of predator trait evolution on the community dynamics. We found that like a slowly switching predator, trait evolution can select for short- and long-term apparent mutualism (Schreiber et al., 2011), but, unexpectedly, prey coexistence depends on the underlying genetic architecture of the predator's attack rates (Schreiber et al., 2018). When predators' switching is adaptive so that predators instantaneously maximize their per capita population growth rate (i.e., a proxy for fitness), dependence of predators' preference for a prey is a discontinuous function of prey abundances. The resulting population dynamics are then described by differential equations with a discontinuous right-hand side, for which solutions are defined in the Filippov sense (because solutions in the usual sense do not exist for control systems with a bang-bang control, e.g., van Baalen et al., 2001; Křivan, 2003, 2006). More broadly, Holt (1977) continues to inspire both of us to dig deep into mathematical models of intermediate complexity while keeping the full complexity in view. We are sure that it will keep inspiring theoretical population biologists for years to come.

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