



## Commentary

## The evolution of coexistence theory

Priyanga Amarasekare

Department of Ecology and Evolutionary Biology, University of California Los Angeles, United States of America

## ARTICLE INFO

## Article history:

Received 8 May 2019

Available online 8 October 2019

## Keywords:

Coexistence

Environmental variation

Invisibility

Storage effect

Relative non-linearity

Permanence

Species coexistence in variable environments is an issue at the heart of all aspects of ecology. Mathematical theory has been crucial in developing a mechanistic understanding of this problem. Theoretical Population Biology has the distinction of being the point of dissemination for many seminal papers on this topic. It is fitting therefore, on this fiftieth anniversary of the journal, to look back at the key milestones in the evolution of coexistence theory. It is also fitting to acknowledge the singular role that Peter Chesson, long-time TPB editor and contributor, has played in elevating this theory to the general rigorous and empirically testable framework that it is today.

The importance of environmental variation in mediating species coexistence has long been appreciated in ecology. However, it was not until the latter part of the twentieth century that the key elements of the mathematical theory were formulated. The 1980s saw the publication of several important papers in TPB (Abrams, 1984; Chesson, 1985) and elsewhere (Armstrong and McGehee, 1980; Chesson and Warner, 1981; Warner and Chesson, 1985; Chesson, 1990). Chesson and Warner (1981) and Chesson (1985) elucidated the role of different types of abiotic environmental variability (temporal, spatial, spatiotemporal) using the lottery model of preemptive competition. Armstrong and McGehee (1980) showed that intrinsically generated consumer-resource fluctuations provide a form of resource partitioning, arising from differential non-linearity in consumers' functional responses, that can allow multiple consumer species to coexist on a common resource.

Peter Chesson's 1994 TPB paper constitutes a crucial milestone in the development of coexistence theory. Chesson used an elegant mathematical analysis to present a general model for multi-species coexistence in variable environments. Although a

body of theory had been accumulating on variation-mediated coexistence (e.g., Abrams, 1984; Armstrong and McGehee, 1980; Chesson, 1985), there was no general theory that could integrate the various theoretical findings within a common mathematical framework. The seminal contribution of Chesson (1994) was to show that all mechanisms of coexistence and exclusion were included within three broad categories. The first encompasses all classical coexistence mechanisms that can occur in the absence of environmental fluctuations (e.g., resource partitioning). The second and third are fluctuation-mediated mechanisms that are distinctively different. The storage effect involves species differing in their responses to environmental variation such that they are limited mostly by intra-specific competition when the environment is favorable to them, and by inter-specific competition when the environment is favorable to their competitors. The "storage" of the fitness benefits accrued during favorable environmental periods allows species to tolerate competition from other species and to weather unfavorable environmental periods. The third mechanism, relative non-linearity, involves competing species differing in their responses to a limiting resource that fluctuates over time (where fluctuations are a response to abiotic environmental variation or a result of the resource's interaction with a consumer species). Importantly, while each mechanism can allow coexistence in the absence of the others, it is also possible for more than one of these mechanisms to operate simultaneously. Because the three mechanisms differ in qualitatively distinct ways, it is not only possible to identify which mechanisms are operating but also to quantify their relative contributions (Chesson, 1994). This framework for partitioning coexistence mechanisms and quantifying their relative contributions have withstood the test of time, and indeed provide the cornerstones of coexistence theory as we know it today.

E-mail address: [amarasek@ucla.edu](mailto:amarasek@ucla.edu).

An important implication of Chesson (1994) was that – contrary to conventional wisdom – harshness, disturbance and fluctuating environments did not lead to coexistence because they could not generate stabilizing mechanisms by which species would limit themselves more than they would others. Exploration of this idea led to another seminal contribution by Chesson and colleagues. In a 1997 paper published in the *American Naturalist*, Chesson and Huntley (1997) showed that environmental harshness cannot in itself influence coexistence in the absence of niche differences, and that environmental fluctuations can favor coexistence only when they generate opportunities for spatial or temporal niche partitioning. An important insight to emerge from this paper is the use of natural scaling relationships between key parameters (e.g., growth rate, generation time) to compare species' long-term growth rates. This idea was fully developed later in Chesson's 2003 TPB paper (Chesson, 2003). This paper presents a technique for partitioning long-term growth rates into community average measures of stabilizing mechanisms, deviations from these measures, and other factors. It is shown that the community average mechanism is the key to quantifying the degree to which a given mechanism can lead to stable coexistence of interacting species. The combination of keen biological insight and mathematical elegance in this partitioning mechanism is reminiscent of the Price Equation in evolutionary biology, a general mathematical theory for selection that is amenable to reasoning about other complex biological problems (Price, 1970; Frank, 1995).

The first decade of the 21st century was a crucial period during which the key elements of the present-day coexistence theory came into being. In an important TPB paper published in 2000, Chesson (2000a) built on the key elements of coexistence theory in temporally variable environments to develop a general framework for competitive and apparent competitive interactions in spatially variable environments. This paper showed that species used similar mechanisms to partition niches in space as do to partition niches in time, i.e., there is a spatial equivalent of storage effect and relative non-linearity. However, the spatial mechanisms involved different life history traits that made coexistence via spatial storage effect more likely than the temporal storage effect but spatial non-linearity less likely than temporal non-linearity. An important finding was that additional mechanisms could arise in the spatial case via the covariance between growth rate and abundance (Chesson, 2000a), an idea expounded in several later papers (Snyder and Chesson, 2004; Snyder et al., 2005). Nowhere was the power of these ideas made more apparent than in the 2000 paper by Chesson in the *Annual Review of Ecology and Systematics* (Chesson, 2000b). This paper, one of the most widely cited in the field of ecology, made several sophisticated mathematical concepts developed in Chesson (1994) accessible to a wider audience, not the least among which was the contrast between stabilizing vs. fitness-equalizing mechanisms, ideas that were later popularized by the neutral theory of ecology (Hubbell, 2000).

As is the case with most mathematical theory, the very rigor of Chesson's work also made it inaccessible to empirical ecologists, thus hampering experimental tests of its predictions. The mid 2000s saw a turning point in this impasse. A series of papers by Chesson and colleagues, which tested the key assumptions and predictions of variation-mediated coexistence mechanisms in the field (Melbourne and Chesson, 2005; Davies et al., 2005; Melbourne and Chesson, 2006; Sears and Chesson, 2007; Angert et al., 2009; Holt and Chesson, 2014), made for the integration of theory and data that had been missing up to that point. These studies involved quantifying the spatial storage effect in plant communities (Davies et al., 2005; Sears and Chesson, 2007), elucidating the role of functional trade-offs in storage effect-mediated

coexistence (Angert et al., 2009), and investigating the interaction between local non-linear dynamics and spatial heterogeneity in aquatic invertebrate communities (Melbourne and Chesson, 2005, 2006).

Buoyed by the empirical findings that served as refinement of the theory, several conceptual advances followed. Up until the 21st century, coexistence had largely been considered in the context of competition. In nature however, species engage in interactions other than competition. The impact of trophic interactions (herbivory, predation, parasitism) on competition, although well-known, had not been incorporated into investigations of coexistence in variable environments. In a series of papers, Chesson and colleagues presented a general mathematical framework for elucidating the conditions for coexistence in the presence of predation (Chesson and Kuang, 2008; Kuang and Chesson, 2008, 2010). In an important paper published in TPB, Kuang and Chesson (2010) showed that when annual plant species in seasonally varying environments experience frequency-dependent seed predation, the interaction between the storage effect and frequency-dependent predation can lead to nonintuitive outcomes. The crucial insight to emerge is the antagonistic effects that predation has on competitive coexistence. On the one hand, predation can reduce the strength of competition-based coexistence mechanisms such as the storage effect by minimizing the difference between intra- and inter-specific competition; on the other hand, strong frequency-dependent predation can itself promote coexistence, thus compensating for the negative consequences of predation on the coexistence via the storage effect.

Most ecological coexistence mechanisms are developed without regard to evolutionary considerations. In a crucial departure from the norm, Mathias and Chesson (2013) investigated the evolutionary stability of coexistence via the temporal storage effect. They found that ecological coexistence was possible in simpler environments but not evolutionarily stable but that increased complexity in environmental variability made for coexistence that was both ecologically and evolutionarily stable. These findings were complemented by parallel studies on the evolution of the storage effect (Snyder and Adler, 2011; Abrams et al., 2013).

More recent TPB papers (Yuan and Chesson, 2015; Stump and Chesson, 2017) have revisited the relative importance of the storage effect and relative non-linearity in coexistence, using techniques that can quantify the separate contributions of the two mechanisms when they are acting in concert. This is an important conceptual advance that allows experimentalists to quantify the absolute and relative strengths of multiple coexistence mechanisms that operate simultaneously (Yuan and Chesson, 2015; Stump and Chesson, 2017). More recent studies (e.g., Letten et al., 2019; Zepeda and Martorell, 2019) have utilized Ellner et al.'s (Ellner et al., 2016) simulation-based approach to investigate coexistence via the simultaneous operation of the storage effect and relative non-linearity.

Nearly all mathematical treatment of coexistence theory in variable environments is based on invasibility analysis, which quantifies species' ability to increase from initially small numbers when their competitors and predators are at their steady-state (or quasi-steady state) abundances. Amongst the potential drawbacks of this approach is that it applies only when the resident species are at equilibrium at the time of invasion (Carroll et al., 2011; Grainger et al., 2019) and has limited generality in multi-species settings where the potential for multiple stable states introduce thresholds below which species cannot increase when rare (Saavedra et al., 2017). In its most recent advance, coexistence theory utilizes new developments in permanence and stochastic persistence to demonstrate the critical role that mutual invasibility criteria play in elucidating the conditions for species coexistence in variable environments (Chesson, 2018).

Thirty years since its inception, and through many influential contributions published in TPB, we have today a theory for coexistence in variable environments that is rigorous in its formulation and empirically accessible in the testing of its predictions. What used to be confined to theoretical journals is now textbook material that undergraduates routinely study in their upper division courses (Begon et al., 2005). Coexistence theory has evolved, not into a static paradigm but a dynamic and vibrant research program that is continually adapting and evolving as the world around us changes and the planet's biota experience new realms of environmental variability.

## Acknowledgments

I thank two anonymous referees for helpful comments that improved the manuscript. This work was supported by the National Science Foundation grant DEB-1457815.

## References

- Abrams, P., 1984. Recruitment, lotteries and coexistence in coral reef fish. *Am. Nat.* 123, 44–55.
- Abrams, P., Tucker, C., Gilbert, B., 2013. Evolution of the storage effect. *Evolution* 67, 315–327.
- Angert, A., Huxman, T., Chesson, P., Venable, D., 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl. Acad. Sci. USA* 106, 11641–11645.
- Armstrong, R., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 115, 151–170.
- Begon, M., Harper, J., Townsend, C., 2005. *Individuals, Populations and Communities*. Blackwell Science, Oxford.
- Carroll, I., Cardinale, B., Nisbet, R., 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92, 1157–1165.
- Chesson, P., 1985. Coexistence of competitors in spatially and temporally varying environments. *Theor. Popul. Biol.* 28, 263–287.
- Chesson, P., 1990. MacArthur's consumer-resource model. *Theor. Popul. Biol.* 37, 26–38.
- Chesson, P., 1994. Multispecies competition in variable environments. *Theor. Popul. Biol.* 45, 227–276.
- Chesson, P., 2000a. General theory of competitive coexistence in spatially varying environments. *Theor. Popul. Biol.* 58, 211–237.
- Chesson, P., 2000b. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366.
- Chesson, P., 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theor. Popul. Biol.* 64, 345–357.
- Chesson, P., 2018. Updates on mechanisms of maintenance of species diversity. *J. Ecol.* 106, 1773–1794.
- Chesson, P., Huntley, N., 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* 150, 519–553.
- Chesson, P., Kuang, J., 2008. The interaction between predation and competition. *Nature* 456, 235–238.
- Chesson, P., Warner, R., 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117, 923–943.
- Davies, K., Chesson, P., Harrison, S., Inouye, B., Rice, K., 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86, 1602–1610.
- Ellner, S., Snyder, R., Adler, P., 2016. How to quantify the temporal storage effect using simulations instead of math. *Ecol. Lett.* 19, 1333–1342.
- Frank, S., 1995. George prices contributions to evolutionary genetics. *J. Theoret. Biol.* 175, 373–388.
- Grainger, N., Letten, A., Gilbert, B., Fukami, T., 2019. Applying modern coexistence theory to priority effects. *Proc. Natl. Acad. Sci. USA* 116, 6205–6210.
- Holt, G., Chesson, P., 2014. Variation in moisture duration as a driver of coexistence by the storage effect in desert annual plants. *Theor. Popul. Biol.* 92, 36–50.
- Hubbell, S., 2000. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- Kuang, J., Chesson, P., 2008. Coexistence of annual plants: generalist seed predation weakens the storage effect. *Ecology* 90, 170–182.
- Kuang, J., Chesson, P., 2010. Interacting coexistence mechanisms in annual plant communities: frequency-dependent predation and the storage effect. *Theor. Popul. Biol.* 77, 56–70.
- Letten, A., Dhami, M., Ke, P.-J., Fukami, T., 2019. Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proc. Natl. Acad. Sci. USA* 115, 6745–6750.
- Mathias, A., Chesson, P., 2013. Coexistence and evolutionary dynamics mediated by seasonal environmental variation in annual plant communities. *Theor. Popul. Biol.* 84, 56–71.
- Melbourne, B., Chesson, P., 2005. Scaling up population dynamics: integrating theory and data. *Oecologia* 145, 179–187.
- Melbourne, B., Chesson, P., 2006. The scale transition: scaling up population dynamics with field data. *Ecology* 87, 1478–1488.
- Price, G.R., 1970. Selection and covariance. *Nature* 227, 520–521.
- Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J.B., Levine, J.M., 2017. A structural approach for understanding multispecies coexistence. *Ecol. Monograph* 87, 470–486.
- Sears, A., Chesson, P., 2007. New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology* 88, 2240–2247.
- Snyder, R., Adler, P., 2011. Coexistence and coevolution in fluctuating environments: can the storage effect evolve? *Am. Nat.* 178, E76–84.
- Snyder, R., Borer, E.T., Chesson, P., 2005. Examining the relative importance of spatial and nonspatial coexistence mechanisms. *Amer. Nat.* 166, E75–E94.
- Snyder, R., Chesson, P., 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *Amer. Nat.* 164, 633–650.
- Stump, S., Chesson, P., 2017. How optimally foraging predators promote prey coexistence in a variable environment. *Theor. Popul. Biol.* 114, 40–58.
- Warner, R., Chesson, P., 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125, 769–787.
- Yuan, C., Chesson, P., 2015. The relative importance of relative nonlinearity and the storage effect in the lottery model. *Theor. Popul. Biol.* 105, 39–52.
- Zepeda, V., Martorell, C., 2019. Fluctuation-independent niche differentiation and relative nonlinearity drive coexistence in a species-rich grassland. *Ecology* 100, E76–84.