PERENNIAL PLANT MODELS TO STUDY SPECIES COEXISTENCE IN A
VARIABLE ENVIRONMENT

by

Chi Yuan

_____

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements

For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2014

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Chi Yuan, titled Perennial Plant Models to Study Species Coexistence in a Variable Environment and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

_____ Date: (12/01/2014)
Peter Chesson

_____ Date: (12/01/2014)
Judith L. Bronstein

_____ Date: (12/01/2014)
Michael L. Rosenzweig

_____ Date: (12/01/2014)
D. Lawrence Venable

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

_____ Date: (12/01/2014)
Dissertation Director: Peter Chesson

STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of the requirements for an advanced degree at the University of Arizona and is deposited in the University Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that an accurate acknowledgement of the source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his or her judgment the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Chi Yuan

ACKNOWLEDGEMENT

I would not have finished my dissertation without the help of many people. I am most grateful for my advisor Peter Chesson. Peter provided me the opportunity to study abroad; he taught me how to be a good scholar and helped me to bridge the culture gap. Peter always thinks differently, sees the fundamentals, and offers sharp advices. He was very patient with my slowly improving academic and writing skill. His high standards always kept me motivated to improve myself. Peter also generously hosted my visits to Tucson in the later stages of the PhD program, after I had moved to Sunnyvale, CA.

I also feel grateful to have had a wonderful committee. Judie Bronstein is a very inspiring mentor, and helped me with an interesting field study during my rotation. Judie always helped me to see the broad picture in my dissertation, and to figure out the research questions that really matter. Her immediate feedback on my manuscripts helped me to seize the fundamentals of my research and communicate more efficiently in my writing. Mike Rosenzweig is an eminent figure, full of wisdom, and very enthusiastic and encouraging. Mike has many novel research ideas. He often surprised me with questions, and stimulated me to think out of the box and be bold in expressing my ideas. Larry Venable is wise and super knowledgeable, and has a strong sense of humor. Larry's broad research on the life history and physiology of desert annuals has been inspiring for formulating my models. I also want to thank all my committee for patiently listening to and reading through my broken English, and still figuring out what I was trying to say.

I feel grateful to Jim Cushing for mentoring and funding me to study the evolution of Allee effect in a stage structured model, and being an extremely supportive and encouraging advisor. I also want to thank Brian McGill for helping me on another rotation study, and showing me how wonderful statistics are. Bob Smith helped me around Desert Station during my preliminary field work there. Ray Turner shared data from an amazing long-term study of desert perennials, and Joseph Wright shared data from an amazing long-term study of tropical forest seedling recruitment. I hope that one day my model can make direct links to these studies.

Everyone in the Chesson Lab, Danielle Ignace, Jessica Kuang, Lina Li, Andrea Mathias, Galen Holt, Yue (Max) Li, Pacifica Sommers, Simon Stump, Nick Kortessis, Stephanie Hart, Krista Robinson, and Elieza Tang, offered me countless help, stimulating conversations, and fruitful feedback for my research. Friends from the department, especially Guan-Zhu Han, Jin Wu, Ginny Fizpatrick, Sara Felker, Jonathan Horst, Lindsey Sloat, Will Driscoll, always gave me lots of feedbacks and encouragements. Thank you to Liz Oxford, Lili Schwartz, Carole Rosenzweig, Sky Dominguez, Lauren Harrison, Pennie Liebig, and Barry McCabe for helping me with the business end of grad school, and making my life much easier. I would also like to thank my funding sources: Science Foundation Arizona; an NSF-funded RA from Jim Cushing; an NSF-funded RA from Peter Chesson; summer research stipends from the department, travel grants from GPSC, Institute of Environment, and HE Carter travel award.

Last but not least, I want thank my friends and family. Thank you for the wonderful Chinese friends I met in Tucson, in particular Ding Ding, Muhua Wang, and Muhan Zhou, for all of your help, and for your friendship. Linda and Rick Hanson treated Li and myself like family. My parents Ying Yu and Jianzhong Yuan, have always been the strongest support for me to carry on. A special thank you to my fiancé Li Fan who has been with me through every challenge I faced to get my PhD.

Dedication
To my parents Ying Yu, Jianzhong Yuan and my fiancé Li Fan for all the love and encouragements.

Table of Contents

List of Figures

Abstract

Living organisms face a changing physical environment. A major challenge in ecology is understanding the ecological and evolutionary role that this changing physical environment has in shaping a community. One fundamental question is how environmental variation affects species coexistence. Modern understanding of environmental variation emphasized the hypothesis that possible adaptations to a fluctuating environment allow species to use different environments in different ways. Species can partition temporally their use of resources. Persistent stages in the life cycle such as prolonged longevity can buffer species through unfavorable environments. Differences in longevity will also lead to different nonlinear responses of population growth rate to fluctuating in resources. Questions arise: how do these possible adaptations to environmental fluctuations affect coexistence. Do they act through multiple coexistence mechanisms, how strong are the mechanisms, and do the mechanisms interact?

A framework has been developed for quantifying coexistence mechanisms in models. Being able to quantify coexistence mechanisms in the field is critical to understand different processes contributing to species coexistence in a community: whether a process prevents species dropping out of the community (stable coexistence), or slows down species losses (unstable coexistence), or both. In many respects, applications of those techniques for quantifying coexistence mechanisms have the potential for substantial improvements. In particular, very few studies directly quantify coexistence mechanisms for perennial plants. Coexistence of plant is often puzzling because they share similar resources. Environmental variation has been suggested as an important factor for niche

partitioning but challenges for studying it in perennial plants are unclear. The long generation time poses challenges to controlled experiments. Moreover, perennial plants have complex life histories. Vital rates change with size. In addition, tremendous temporal variation is observed in various life history processes. Seedling recruitment and individual growth can both be highly sensitive to fluctuation in the physical environment. Furthermore, different processes in different stages of the life history can interact with environment and competition in different ways. Using perennial plants as a specific system, our study reveals a crucial role in theory development to summarize understanding of such a complex system. I start with the simplest model for perennial plants, the lottery model, to study the relative importance of two coexistence mechanisms: the storage effect and the relative nonlinearity. Then I extend the model by showing that variation in individual growth can also lead to stable coexistence similar to the effect of variation in seedling recruitment. Species can benefit most from variable environments when the processes contributing most to capturing resources on average are also very sensitive to environmental fluctuations. New mechanisms arise through shifts in size structure, which depend on how vital rates change through ontogeny.

Introduction

A central question in community ecology is why there are so many species. Many studies are devoted to understanding patterns in biodiversity: its origin, maintenance and loss. Interests in biodiversity have been driving rapid development of coexistence theories. Early work on the Lotka-Volterra competition model predicts that the number of density dependent limiting factors must be equal to or greater than the number of coexisting species. This theoretical finding is challenged by the empirical observation in many systems (especially plant communities) that many species coexist although few limiting resources are evident. Many hypotheses have been proposed to explain species coexistence. Palmer (1994) reviewed and classified these hypotheses into different categories in terms of how they violate different conditions for coexistence in Lotka-Volterra competition models. Many of these hypotheses are synonyms or near synonyms. Though these classifications are problematic in light of modern understanding of coexistence mechanisms (Chesson 2000), this review is helpful in highlighting the important role in species coexistence of temporal and spatial variation, which is absent from Lotka-Volterra models.

There have been many theoretical studies on the role of environmental variation in species coexistence. An early study claimed that environmental variation prevents species from remaining at equilibrium and promotes species extinction (May 1973, 1974). However, environmental variation, rather than being treated as a disruptive force for ecological processes, should be treated as part of the ecosystem (Chesson at al 2013). More recent studies, now widely accepted, come to the conclusion that environmental variation promotes species coexistence by offering new ways in which species can be

differentiated ecologically. These studies extend the classical niche concept developed

with Lotka-Volterra models to include responses to variable environments as part of the

niche (Chesson 1991). For example in plant communities, without environmental

variation, niche overlaps are mediated by the way species relate to resources and

predators. Spatial and temporal environmental variation offers species opportunities to be

relative specialists on different environmental conditions, reducing interactions with other

members of the same ecological guild.

Several fluctuation-dependent mechanisms, which by definition are mechanisms that

depend on fluctuations in population densities and environmental factors in space and

time, have been proposed as promoting stable coexistence in a community (Clements

1916, Hastings 1980, Pacala and Tilman 1994, Amarasekare and Nisbet 2001, Tilman

2004). I will explain two hypotheses as examples here. Competition-colonization

tradeoffs are one popular hypothesis for multispecies coexistence on a single resource

(Tilman 1994). This theory has been criticized because of its strict requirements on

interspecific trade-offs between competitive ability, and colonization ability, as well as a

fixed hierarchy of these abilities (Yu and Wilson 2001). Two other related popular

hypotheses are the regeneration niche (Grubb 1977) and the gap dynamics hypothesis

(Grubb 1977, Denslow 1987). New gaps after tree death open a range of microhabitats,

allowing species with different regeneration requirements to establish. It has been further

suggested that climate variation associated with gap formation will tend to favor different

species at different times and allow an occasional match between seedling availability of

different species and gap formation (Runkle 1989). However, this theory has been

criticized because a limited number of species dominate regeneration in gaps, leaving

unexplained regeneration and coexistence of the majority of tropical forest trees, which are shade tolerant, slow growing and normally excluded by other species upon gap formation (Wright 2002).

However, none of these above hypotheses consider life history characters such as species-specific responses to environments as possible adaptations to a variable environment. Nor did they seriously study the role of a variable environment in promoting recovery of species from low density (i.e. invasibility), which is essential to quantify the strength of stable coexistence. For a species to recover from low density, it must have a demographic advantage at low density. One way of achieving this is through species-specific responses to varying environmental conditions (Chesson and Warner 1981). However, differences between species are not sufficient for species coexistence, and the critical issue lies between how species differences interact with density-dependent process to promote rare species advantages (Chesson 2000, 2008, Siepielski and McPeek 2010).

Different aspects of life history can lead to specific density-feedback loops for a species resulting in stronger intra- than inter-specific competition on some spatial and temporal scale. Chesson (2003, 2008) argues that these different effects are best understood through partitioning the low density advantages into quantifiable coexistence mechanisms. The lottery model is the simplest model used to quantify coexistence mechanisms in a temporally varying environment (Chesson 1981). Two coexistence mechanisms arise in the model: the storage effect and relative nonlinearity. In brief explanation, the storage effect arises through an interaction between environment and competition: species at low density have opportunities to escape competition in a

favorable environment, and suffer less from competition in an unfavorable environment (Box 1). Relative nonlinearity arises because species have different nonlinear response to competition and thus are affected in different ways by fluctuations in competition (Box 2).

Quantification of the mechanisms allows identification of critical life history processes for the mechanisms. Several critical questions are: how do the life histories affect the relative importances of different coexistence mechanisms that are present together in the system? Are important life history processes for species coexistence missing in previous studies? Most theoretical and empirical work focuses on the storage effect. Among these studies, most have focused on recruitment stages. So the questions here remain open.

Box 1**. The Storage Effect**

Quantification of coexistence mechanisms is done in the context of invasion analysis: one species is perturbed to low density and is termed the invader species, and the rest of the species converging on stationary fluctuations are termed residents. The storage effect is often the strongest mechanisms under temporal variation because its two key requirements can be met most easily (Chesson 2003). 1) **Weaker (relatively negative) covariance between environment and competition for invader species compared with residents** (Fig. 1). Resident species are predicted to often have strong positive covariance. This means that they will not benefit much from a favorable physical environment because the potential recruitment from the favorable physical environment is reduced by strong competition. In contrast, the invader species will enjoy an advantage when favorable environments coincide with low competition. For example, if the species respond to the physical environment in different ways, when the invader is favored by the

physical environment, the resident might not be. Since the resident is the cause of most competition, the invader can escape competition when it's favored by the physical environment, and so take full advantage of these favorable conditions. 2) **Buffered population growth as a result of persistent stages in life cycle**. With a persistent stage that helps a species to survive through years of bad recruitment, recruitment gains in favorable years will not be offset by population decline in bad years. Perennial plants meet this requirement by having a long life span, allowing persistence through bad years of environment and competition.
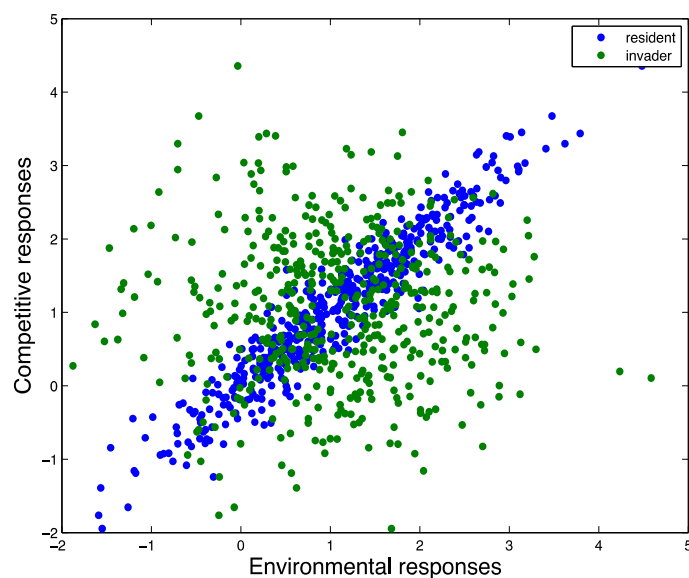

Figure 1. Covariance between environment and competition: comparison between resident (blue dots) and invader species (green dots). For resident species, strong intraspecific competition accompanies a favorable environment, resulting in strong positive covariance. Invader species here have independent environmental responses from resident species as illustrated in this graph. Covariance is low for the invader because the invader can enjoy a favorable environment with low competition when resident is in an unfavorable environment.

Indeed, assumptions for the storage effect (Box 1) can be easily met in recruitment of various systems. The temporal storage effect has been explored in variety systems such as freshwater zooplankton, desert annuals, prairies and forests (Pake and Venable 1995, Cáceres 1997, Kelly and Bowler 2002, Adler et al. 2006, Angert et al. 2009, Usinowicz et

al. 2012). Strong recruitment variation has often been observed in all these systems. For example, germinations of desert annual species are highly species-specific in relation to rainfall and temperature (Chesson 2013, Angert 2009, Kimball 2012). Prairie grasses shows contrasting correlations between intrinsic growth rate and climate variables (Adler 2006). Even in tropical forest where environment variation is generally regarded small, there is dramatic variation in seedling recruitment (Wright 2005). Also common cross all systems, organisms either are long-lived or have a dormant stage to buffer themselves against unfavorable environments.

While there is sufficient evidence for assumptions of storage effect to hold across these systems, these same evidences do not preclude the existence of other mechanisms. Fluctuating environments drive fluctuation in competition; life history traits such as longevity and persistence in the seed bank that lead to the buffer required by the storage effect. When different between species, these buffers also drive different nonlinear responses to competition between species (Box 2). These two conditions of the relative nonlinearity are inseparable from conditions that lead to the storage effect. Even though both mechanisms are generally present together, the storage effect is usually the only mechanism being investigated. Part of the ignorance is due to an unclear expectation of when relative nonlinearity is important. To make up this gap in understanding, in the Appendix A of the dissertation, I use the simple lottery model to provide a quantitative assessment to compare the two coexistence mechanisms functioning together in a temporally variable environment. This work provides a foundation for understanding how life history traits (e.g. longevity, fecundity, sensitivities and correlations in environmental responses) affect the relative importance of the coexistence mechanisms. It clearly

identifies conditions when relative nonlinearity can be strong, and conditions when negligence can be justified.

Even though I have been emphasizing the need to investigate multiple mechanisms, even for storage effect alone, direct empirical test can be challenging. Very few studies (Chesson 2008) directly measured the key functional component of the storage effect, covariance between environment and competition (covEC). This covariance has been estimated directly in studies of spatial storage effect (Sears and Chesson 2007) by direct manipulation of a species' density in a neighborhood competition experiment. While such manipulation may not be feasible in all situations, for the temporal storage effect there is an extra-layer of difficulty in the time-scale of the experiment. It can be problematic if the species studied have a slow life cycle. For this reason, quantification of temporal storage effect is often done indirectly via models. For example, in studies of the temporal storage effect in desert annuals, the connection between environmental variation and species interactions is derived from long term demographic data based on the assumption of lottery competition, without directly measuring competition (Angert et al. 2009, Chesson et al. 2011). Questions arise, does our conclusion about the strength of mechanisms depends the sort of model used?

Box 2 Relative nonlinearity

Relative nonlinearity depends on species' relatively nonlinear responses to the fluctuations in limiting resources (Fig. b1). Because of these differences, species will benefit in different ways from fluctuations in the limiting factors (Chesson 2000). Based on Jensen's inequality, species

with a growth rate that curves up more strongly as a function of competition, will benefit from larger fluctuations. For coexistence to be promoted, this species must experience stronger fluctuations as an invader than does the other species as an invader. It is potentially important in a system where there are strong associations between the strength of nonlinearity and the strength of population fluctuations. The key in testing relative nonlinearity lies in calculating the variances of competitive responses and nonlinearity differences. This is difficult in the field studies because direct estimation of nonlinearities is difficult. Thus there is need for theory to provide a clear expectation of when relative nonlinearity is important. In a discrete-time population growth model, nonlinearities can simply arise from life-history traits, such as adult survival in lottery model.
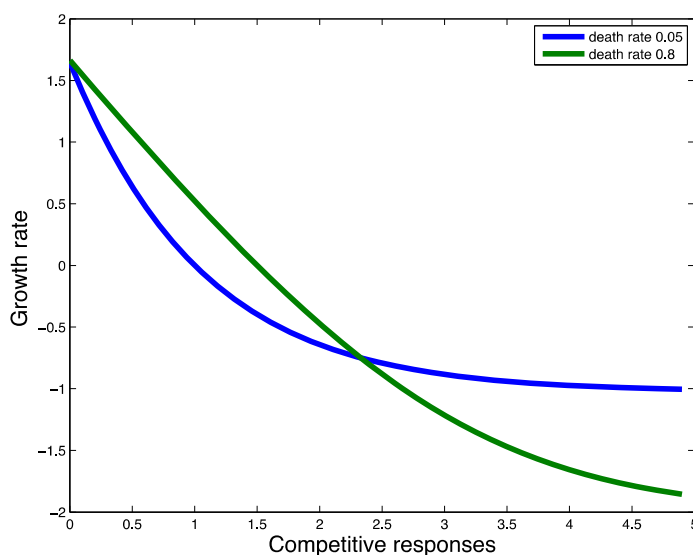

Figure 2. Relative nonlinearity response of growth rate to competition. In the lottery model, relative nonlinearity simply arises from longevity differences between species. The growth rate as response to competition for longer lived species (blue line) is more convex than shorter lived species (green line). Longer lived species benefit more from fluctuations in competitive responses than shorter lived species.

The key models used to develop theories on the role of environmental variation in species coexistence have been relatively simple, which makes them more tractable and understandable. Nevertheless, simple models do not necessarily match empirical systems

very well. For example, the lottery model, unlike abstract models such as Lotka-Volterra model, does have important life history explicitly represented. Yet it is still a serious contraction of the life history. The basic lottery model differentiates individuals between two states only: propagule and adults. Critical processes including reproduction, propagule competition, and establishment as adult occur in one unit of time.

While the basic model has focused on recruitment stages, post-recruitment dynamics can also be interesting. Details such as how fast an individual grows, at what stage it starts to reproduce, and how reproduction and mortality change with size reflect much about how life history strategies between species differ. Moreover, it is likely that environment and competition can shape the post-recruitment stages no less than their influence on recruitment variation. Using a forest as an example, trees are always resource limited, in particular by light. Saplings are inferior in competition for light and can stay small for an extended period before reaching the threshold of reproduction. However, individual growth of the trees of different species can be favored by different climate conditions. The rapidity of individual growth responses to favorable conditions varies between species. Simple models may fail to capture these detailed life-histories of a real system, but dothese life history details appreciable affect the strengths of coexistence mechanisms?

To answer this question, I built a size-structured model that can capture more interesting biology. In Appendix B of the dissertation, I develop a continuous size-structured lottery model and use it to summarize the effect of a complex life history on species coexistence. Continuing in Appendix C, I use this model to study coexistence of species with life-history contrasts in reproduction and growth. This new model allows me

to answer more biologically relevant questions. The model shows temporal variation in multiple life history traits can lead to stable coexistence. Temporal variation further leads to dynamic size structure for each species and this fact reveals new insights into how size-dependent life-history schedules shape community structure.

Present study

Research done in this dissertation is presented as three manuscripts in Appendix A, B and C. A central theme of the dissertation is developing models and theory that can facilitate better understanding of species coexistence in a temporally varying environment. My studies develop around the lottery model and its enhancement, the size-structured lottery model. The lottery model is used to study iteroparous perennial organisms. I have illustrated the model using forest trees and developed the model with strong intention for better match with empirical studies in forests. Progressing from the simple model to the more enhanced size structured model, I am able to investigate different aspects of life history and the different coexistence mechanisms they affect. Together, three studies provide answers to questions that need to be asked in every study of species coexistence: which coexistence mechanisms are operating, how important these mechanisms are, and how the different mechanisms interact. Below I summarize the major foundings in each appendix.

Appendix A is in revision with Theoretical Population Biology. This study uses the lottery model to explore when relative nonlinearity is important. In the lottery model, the relatively nonlinear growth rates arise simply from death rate differences. As a direct consequence, species are favored in different ways as resources fluctuate. There is stronger nonlinearity in population growth of longer-lived individuals as a function of resources. A species' longevity helps it persist through strong competition. Based on Janzen's inequality, long-lived species are favored by stronger fluctuations in resources than shorter-lived species. For relative nonlinearity to be important, life history traits of

species must have the following characteristics: (1) species must differ greatly in their adult death rates, (2) sensitivity of recruitment to environmental variation must be greater for species with larger adult death rates, and (3) there must be high correlations between species in the responses of recruitment to the environment. When these requirements are met, a long-lived species, when abundant, favors its shorter-lived competitor by reducing fluctuations in competition. A shorter-lived species, when abundant, favors its longer-lived competitors by increasing fluctuations in competition. These requirements for relative nonlinearity to be strong are much harder to satisfy than the requirements for the storage effect (Box 1). Nonetheless, the situations when relative nonlinearity is important are also when storage effect is weak. Relative nonlinearity might have a compensating role for a weak storage effect in nature.

As Appendix A shows, the lottery model has been a powerful tool to quantify the strength of coexistence mechanisms. Yet the basic model has left out an important property of an organism—its size. Size, either for offspring, or adults, has had a prominent role in the formulation of life history strategies (Clark and Clark 1992, Thomas 1996, Westoby et al. 2002, King et al. 2006, Muller-Landau et al. 2006, Iida et al. 2013). Size is closely related to other important properties of trees such as competitive ability, growth rate, fecundity, mortality rate etc. In Appendix B I introduce size into the model. It not only brings in detailed life histories, but also fundamentally changes the structure of the model. While the effect of tree growth dynamics, especially temporal variation of tree growth, on species coexistence is unclear, the new model allows us to explicitly study the post-recruitment individual growth process. I illustrate the model using forest trees. The model works in discrete time, and in each unit of time trees die

and the area they give up is competed for by others. Competition comes from two sources: (1) newly germinated seedlings compete for space to establish; (2) established individuals compete to grow and take up the newly available space. Competition between individuals occurs for this new space according to a lottery formula: the allocation of space to an individual is the proportion of its demand for space relative to the total demand from all individuals of all species in the same forest. The demand for space of an individual is species specific, and depends on its size and the environment. Demand for space from reproduction and individual growth can vary separately from year to year in response to environmental variation. Competition reduces the actual seedling establishment and growth of an individual. Growth is a continuous process, unlike the discrete form in matrix models.

In Appendix B, I briefly illustrate the model using a guild of species where mean life history schedules are identical but have species-specific responses to the environment. In Appendix B, I show that general understanding of the coexistence mechanisms does not have to sacrifice detailed biology. The techniques for quantifying species coexistence in simple models can be applied to the more complex model easily. I extend understanding of the storage effect by showing now that variation in individual growth can lead to the storage effect. The relative importance of variation in reproduction and variation in individual growth depends on the average importance of reproduction and individual growth to population growth. Variation in reproduction and variation in individual growth can further interact when present together: a synergistic effect when positively correlated and an antagonistic effect when negatively correlated. Low density advantages in the storage effect lead to a new mechanism through shift in size structure. A shift in

structure can promote or undermine species coexistence depending on whether the size shifts at low density towards individuals having more demographic advantage, which is determined by the totality of the shapes of demographic schedules.

In Appendix C, I further investigate species with contrasting mean life history in addition to species-specific environmental responses. Contrasting life histories potentially carry much information about species differences in ecological strategies. Identifying which aspects of these differences affect species coexistence is a critical task for theory. I illustrate the finding using a pair of species with contrasting fecundity and growth schedules. The two species have a tradeoff in life-time averages in reproduction and growth. They also differ in how life history traits change through ontogeny. Though trade-offs between contrasting life histories are commonly believed to play an important role in species coexistence, few studies have clearly associated them explicitly with quantifiable coexistence mechanisms. Similarly, ontogenetic shifts in reproduction, growth, and survival have much been discussed in the context of life history evolution and population demographics. Less is known about their effects on species coexistence. I provide a quantitative understanding of how such differences in life histories affect species coexistence through different coexistence mechanisms.

In my model, under a constant environment, life-history tradeoffs can affect average fitness-differences between species only, and potentially act as equalizing mechanisms. Shapes of demographic schedules have no effect if their population average mean is fixed. Stable coexistence arises only in a variable environment in our model, but the strength of the stabilizing effect depends on the mean differences between species. Tradeoffs in reproduction and individual growth affect species coexistence through altering the

relative importance of variation in reproduction and variation in individual growth. The storage effect, the main stabilizing mechanism in the model, is strongest when the sensitivity of a life-history process to variation in the environment is aligned positively with the tradeoff between life-history processes. Thus, a species with high environmental sensitivity in fecundity should have an average advantage in fecundity relative to a species with high sensitivity in individual growth, which should have an advantage in individual growth.

Differences in shapes of demographic schedules, on the other hand, affect species coexistence through shifts in size structure. Shifts in structure happen because of low density advantages in recruitment or individual growth brought by the storage effect. The storage effect in reproduction drives the size structure to include more smaller individuals, favoring species whose smaller individuals contribute more strongly to population growth. The storage effect in individual growth drives size structure to include more larger individuals. The effect of shapes in demographic schedules is very limited. An effect is only strong when shifts occur between size ranges differing dramatically in contributions to population growth. For a low density advantage to occur for two species from opposite size dependence in their demographic rates, an opposite shift in size structure is required.

References

Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. F. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proceedings of the National Academy of Sciences of the United States of America **103**:12793-12798.

Amarasekare, P. and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist **158**:572-584.

Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. Proceedings of the National Academy of Sciences **106**:11641-11645.

Cáceres, C. E. 1997. Temporal variation, dormancy, and coexistence: A field test of the storage effect. Proceedings of the National Academy of Sciences of the United States of America **94**:9171-9175.

Chesson, P. 1991. A need for niches? Tree **6**:26-28.

Chesson, P., N. J. Huntly, S. H. Roxburgh, M. Pantastico-Caldas, and J. M. Facelli. 2011. The storage effect: definition and tests in two plant communities.*in* C. K. Kelly, M. G. Bowler, and G. A. Fox, editors. Temporal dynamics and ecological process. Cambrige University Press, In press.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**:343-366.

Chesson, P. L. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical population biology **64**:345-357.

Chesson, P. L. 2008. Quantifying and testing species coexistence mechanisms. Unity in Diversity: Reflections on Ecology after the legacy of ramon margelef.

Clark, D. A. and D. B. Clark. 1992. Life-history diversity of canopy and emergent trees in a neotropical rain-forest. Ecological Monographs **62**:315-344.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation, Carnegie Institution of Washington, Washington, DC.

Denslow, J. S. 1987. TROPICAL RAIN-FOREST GAPS AND TREE SPECIES-DIVERSITY. Annual Review of Ecology and Systematics **18**:431-451.

Grubb, P. J. 1977. Maintenance of species-richness in plant communities - importance of regeneration niche. Biological Reviews of the Cambridge Philosophical Society **52**:107-145.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology **18**:363-373.

Iida, Y., L. Poorter, F. J. Sterck, A. R. Kassim, M. D. Potts, T. Kubo, and T. Kohyama. 2013. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. Ecology.

Kelly, C. K. and M. G. Bowler. 2002. Coexistence and relative abundance in forest trees. Nature **417**:437-440.

King, D. A., S. J. Davies, and N. S. M. Noor. 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. Forest Ecology and Management **223**:152-158.

Muller-Landau, H. C., R. S. Condit, J. Chave, S. C. Thomas, S. A. Bohlman, S. Bunyavejchewin, S. Davies, R. Foster, S. Gunatilleke, N. Gunatilleke, K. E. Harms, T. Hart, S. P. Hubbell, A. Itoh, A. R. Kassim, J. V. LaFrankie, H. S. Lee, E. Losos, J. R. Makana, T. Ohkubo, R. Sukumar, I. F. Sun, N. M. N. Supardi, S. Tan, J. Thompson, R. Valencia, G. V. Munoz, C. Wills, T. Yamakura, G. Chuyong, H. S. Dattaraja, S. Esufali, P. Hall, C. Hernandez, D. Kenfack, S. Kiratiprayoon, H. S. Suresh, D. Thomas, M. I. Vallejo, and P. Ashton.

2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecology Letters **9**:575-588.

Pacala, S. W. and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist **143**:222-257.

Pake, C. E. and D. L. Venable. 1995. Is Coexistence of Sonoran Desert Annuals Mediated by Temporal Variability Reproductive Success. Ecology **76**:246-261.

Palmer, M. W. 1994. VARIATION IN SPECIES RICHNESS - TOWARDS A UNIFICATION OF HYPOTHESES. Folia Geobotanica & Phytotaxonomica **29**:511-530.

Runkle, J. R. 1989. SYNCHRONY OF REGENERATION, GAPS, AND LATITUDINAL DIFFERENCES IN TREE SPECIES-DIVERSITY. Ecology **70**:546-547.

Sears, A. L. W. and P. L. Chesson. 2007. New methods for quantifying the spatial storage effect: An illustration with desert annuals. Ecology **88**:2240-2247.

Siepielski, A. M. and M. A. McPeek. 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology **91**:3153-3164.

Thomas, S. C. 1996. Relative size at onset of maturity in rain forest trees: A comparative analysis of 37 Malaysian species. Oikos **76**:145-154.

Tilman, D. 1994. Competition and Biodiversity in Spatially Structured Habitats. Ecology **75**:2-16.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. PNAS **101**:10854-10861.

Usinowicz, J., S. J. Wright, and A. R. Ives. 2012. Coexistence in tropical forests through asynchronous variation in annual seed production. Ecology **93**:2073-2084.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125-159.

Wright, J. 2002. Plant diversity in tropical forests: a review of mechanisms of species

    coexistence. Oecologia **130**:1-14.

Yu, D. W. and H. B. Wilson. 2001. The competition-colonization trade-off is dead; Long live the

    competition-colonization trade-off. American Naturalist **158**:49-63.

Appendix A

The relative importance of relative nonlinearity in the lottery model

Chi Yuan[1] and Peter Chesson[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, United States

Corresponding author

C. Yuan: cyuan@email.arizona.edu, Ph: (520) 621-1889

P. Chesson: pchesson@u.arizona.edu, Ph: (520) 621-1451

Key word: Recruitment variation; Fluctuation-dependent mechanisms; Variable environment; Stable coexistence; Relative nonlinearity; The storage effect; Stabilizing mechanism; Equalizing mechanism;

Abstract

The coexistence mechanism called relative nonlinearity has been studied most
seriously in deterministic models. However, it is predicted to arise frequently also when
temporal variation has a stochastic origin. For example, it is known that the relatively
nonlinear growth rates on which the mechanism depends arise simply from differences in
life history traits. Many kinds of temporal variation can then interact with these
nonlinearity differences to create the relative nonlinearity coexistence mechanism.
Studies of stochastic models have focused on the storage effect coexistence mechanism,
which is believed to be more important in the presence of temporal environmental
variation, thus overshadowing studies of relative nonlinearity. However, total neglect of
relative nonlinearity is not justified. This is true even for the lottery model of iteroparous
communities in a variable environment, most known for demonstrating the storage effect.
Here, we use the lottery model to provide a much needed quantitative assessment of the
relative and combined effects of relative nonlinearity and the storage effect. We find that
relative nonlinearity is able to contribute substantially to species coexistence in the lottery
model, and in some circumstances is stronger than the storage effect or is even the sole
mechanism of coexistence. Three requirements need to be met for relative nonlinearity to
be stronger than the storage effect: (1) species must differ greatly in their adult death
rates, (2) sensitivity of recruitment to environmental variation must be greater for species
with larger adult death rates, and (3) there must be high correlations between species in
the responses of recruitment to the varying environment. Although these situations may
not be common in nature, partial satisfaction of these requirements can still lead to

substantial contributions of relative nonlinearity to species coexistence even though the storage effect would likely be stronger.

Introduction

Classically, community ecology focused on equilibrium mechanisms, or in modern terminology, fluctuation-independent mechanisms, i.e. mechanisms that can function without fluctuations over time in population densities or environmental variables (Chesson 2000). However, as natural populations do fluctuate, and invariably experience a temporally varying physical environment, it is essential to ask if those fluctuations have a role in species coexistence (Hutchinson 1961). Early work studied the potential roles of stochastic fluctuations in disrupting stable equilibria (May 1973, 1974). However, it was soon realized that temporal fluctuations, whether stochastic or deterministic, might also create coexistence mechanisms (Chesson and Warner 1981, Abrams 1984, Ellner 1984, Shmida and Ellner 1984, Loreau 1992). These types of coexistence mechanism are termed fluctuation-dependent because to function they require fluctuations over time in population densities or environmental variables (Chesson 1994).

A unified theoretical approach to coexistence in temporally varying environments has revealed two broad classes of fluctuation-dependent coexistence mechanism, the storage effect, and relative nonlinearity (Chesson and Warner 1981, Chesson 1994, Chesson 2000, 2008). The storage effect arises from interactions between fluctuations in the physical environment and fluctuations in the intensity of competition. It provides

advantages to a species perturbed to low density by allowing the species to escape competition at times when the environment favors it, but not its competitors. The outcome is recovery from low density and hence species coexistence. The mechanism relative nonlinearity is named from the requirement that different species have different nonlinear responses to competition. If competition fluctuates over time, Jensen's inequality (Needham 1993) means that the long-term growth rates, which are time averages of short-term growth rates, will be affected differently for different species (Armstrong and McGehee 1980, Chesson 2000, Kuang and Chesson 2008). Relative nonlinearity promotes coexistence when species drive fluctuations in competition in directions that favor their competitors.

Coexistence by relative nonlinearity can result from endogenous fluctuations in population densities (Armstrong and McGehee 1980, Adler 1990, Abrams and Holt 2002, Kuang and Chesson 2008, Kang and Chesson 2010) and from external environmental fluctuations that drive fluctuations in population densities (Chesson 1994, Chesson 2000, 2003, 2008). In difference equation models for species with seasonal reproduction, relatively nonlinear growth rates arise simply from differences between species in life-history traits (Chesson 1994, Chesson 2003). In such models, fluctuations in competition are often driven by fluctuations in environmental factors (Chesson 1994), although endogenously driven fluctuations have also been considered (Kuang and Chesson 2008). In both cases, coexistence is possible from relative nonlinearity. When fluctuations in competition are driven by environmental fluctuations, such as in the lottery model studied here, the storage effect is always present too. As the storage effect has been predicted to be the more important coexistence mechanism (Chesson 1994), the role of relative

nonlinearity has often been ignored. Moreover, empirical studies of coexistence in a variable environment have focused almost exclusively on the storage effect even though a reasonable expectation is that relative nonlinearity is present too (Chesson 2003).

Both Chesson (1994) and Abrams and Holt (2002) point out that it is difficult for relative nonlinearity alone to maintain coexistence of more than two species competing for single resource whether fluctuations are endogenous in origin or due to temporal environmental variation. However, Abrams and Holt (2002) show that relative nonlinearity can have a coexistence promoting effect comparable to the resource partitioning in the case of two competing species, and Chesson (2003) suggests that relative nonlinearity might still be important in multispecies systems through its interactions with other mechanisms even though alone it is not effective in stabilizing coexistence of more than two species on one fluctuating resource. The case of relative nonlinearity with multiple resources has not been studied extensively, but general considerations in Chesson (1994) suggest that the complex nonlinearities possible in multiple resource systems have strong potential to promote coexistence. Indeed, one example of relative nonlinearity with multiple resources and endogenous fluctuations was found to strongly promote coexistence of phytoplankton species (Huisman and Weissing 1999, 2002). More study of the potential for coexistence by relative nonlinearity with multiple resources is certainly needed, but no less important is a better understanding the role of relative nonlinearity in the single resource case when other mechanisms are present. As models of recruitment variation that lead to the storage effect coexistence mechanism generally also permit relative nonlinearity, it is essential to understand what the relative contribution of relative nonlinearity to coexistence might be. It is also

important to know if relative nonlinearity can make a strong contribution to coexistence in multiple species cases when other mechanisms are present even though alone is unlikely to permit coexistence of more than two species. Without this understanding, the almost exclusive focus on the storage effect in models of recruitment variation may be seriously misleading.

The purpose of this article is to determine if relative nonlinearity, driven by physical environmental fluctuations, can contribute importantly to species coexistence in comparison with the storage effect in circumstances when both mechanisms would be expected to be found. We use the lottery model for iteroparous perennials, which has been an important model for understanding the role of environmental variation in species coexistence (Chesson and Warner 1981, Comins and Noble 1985, Hatfield and Chesson 1997, Hubbell 2001, Kelly and Bowler 2002). In this model, environmental fluctuations cause recruitment to vary from year to year. Persistent adult stages buffer population growth against unfavorable times, permitting the storage effect to be present. At the same time, species differences in adult death rates enable relative nonlinearity to be present. These features mean that these two mechanisms are nearly always present together and their contributions to coexistence are not independent. Indeed, below we show that important factors contributing to the strength of relative nonlinearity also crucially determine the strength of the storage effect. As parameters are changed, relative nonlinearity often changes in a contrasting way to the storage effect, which makes relative nonlinearity more important when the storage effect is weak. We determine the conditions that allow relative nonlinearity to be stronger than the storage effect. These conditions are identified using approximate formulae for mechanism strength, backed up

by simulations. Our results show that relative nonlinearity has the potential to be important in natural systems, justifying empirical study of this mechanism.

Relative nonlinearity and the storage effect in the lottery model

The lottery model describes community dynamics of iteroparous perennial species. Two distinct life stages, juveniles and adults, are considered. Each year, adults reproduce, and the resulting number of juveniles varies stochastically overtime, driven by the varying physical environment. Juveniles require open space to establish and mature as adults. Space is assumed to be limited, becoming available only with adult death. Juveniles compete for this space to recruit as adults. Success of a species in this competition for space is assumed proportional to the total number of juveniles produced during a given recruitment period. After maturation to an adult, the survival of an individual is assumed to be insensitive to both the varying physical environment and competition.

The lottery model has been used for perennial plants such as forest trees, and marine space holding organisms such as coral reef fishes or benthic invertebrates (Chesson and Warner 1981, Chesson 1994, Pacala and Tilman 1994, Kelly and Bowler 2002, Munday 2004). The model is in fact closely related to the model commonly used in neutral theory to define dynamics within a forest stand (Hubbell 2001). However, as implemented here, it is far from neutral.

The model is specified by the following difference equation for the dynamics of *n* perennial species:

$$N_j(t+1) = \left\{ 1 - \delta_j + \left[\sum_{k=1}^{n} \delta_k N_k(t) \right] \frac{\beta_j(t)}{\sum_{k=1}^{n} \beta_k(t) N_k(t)} \right\} N_j(t) \qquad (1)$$

$$j = 1, \; ... \; , \; n$$

Here $N_j(t)$ represents density of species j at time t, δ_j is the adult death rate, which is assumed to be constant over time, and $\beta_j(t)$ is the per capita number of juveniles produced by species j at time t. The recruitment to adults thus depends on per capita reproduction and survival of offspring to the juvenile stage when they compete for space to establish. The vector $\boldsymbol{\beta}(t) = (\beta_1(t),…, \beta_n(t))$ is assumed to vary independently over time, but with components correlated between species. In our simulations, $\boldsymbol{\beta}$ follows a multivariate lognormal distribution with parameters that remain constant over time.

Eq. (1) is a population model of the general form

$$N_j(t + 1) = \lambda_j(t) \, N_j(t) \qquad (2)$$

where $\lambda_j(t)$ is the finite rate of increase, and is here equal to the term in braces in Eq. (1). Eq. (2) represents population growth multiplicatively. To analyze the model, we need to put it on an additive scale, which is the log scale. The logarithm of the finite rate of increase, $r_j(t) = \ln\lambda_j(t)$,

$$r_j(t) = \ln N_j(t + 1) - \ln N_j(t), \qquad (3)$$

has the helpful property that its sum over a given period of time gives the change in $\ln N_j(t)$ for that same period of time. Equivalently, the time average, $\bar{r}_j$, of $r_j(t)$ defines the

average change in $\ln N_j(t)$.

Log scales for various quantities have also been long found to be the simplest scales for understanding the behavior of the lottery model (Chesson 1982, 1994), and in order to place the model in a generic form for studying relative nonlinearity and the storage effect, we define the environmental response of species j as $E_j(t) = \ln\beta_j(t)$, and the competitive response as

$$C(t) = \ln\left\{\sum_{j=1}^{n}\beta_j(t)N_j(t)/\sum_{j=1}^{n}\delta_j N_j(t)\right\}. \qquad (4)$$

Note that in this definition, $\sum_{j=1}^{n}\delta_j(t)N_j(t)$ represents the amount of space available for juvenile settlement in the year t. It is equal to the total space released by adult death. The quantity $\sum_{j=1}^{n}\beta_j(t)N_j(t)$ is the demand for this space in terms of the total density of juveniles competing for this space. The ratio of these two quantities is a measure of the magnitude of competition, which can be understood intuitively as "demand for space" divided by "supply." Eq. (4) puts this quantity on a log scale as $C(t)$. The model can then be written in the following generic form for iteroparous perennial organisms (Chesson 2003):

$$r_j(t) = \ln\left\{1 - \delta_j + e^{E_j(t) - C(t)}\right\}. \qquad (5)$$

This formula distinguishes two life-history processes, adult survival, which occurs with probability $1 - \delta_j$, and recruitment to the adult stage, which occurs at the per capita rate $\exp(E_j(t) - C(t))$.

When δ_j is less than 1, as will always be the case for perennial organisms, $r_j(t)$ is a nonlinear function of the competitive response, $C(t)$. Indeed, it is a convex function of $C(t)$ as can be seen from its positive second derivative in $C(t)$. Because the degree of convexity depends on δ_j, when the δs differ between species, their growth rates differ in convexity, which means they are relatively nonlinear functions. Note also that $C(t)$ fluctuates over time due to the fluctuating environment and fluctuating species densities. Jensen's inequality (Needham 1993) says that the average of a convex function, $\overline{f(C)}$ (= $\overline{r_j}$ here), of a varying quantity C, is greater than the function of the average, $f(\overline{C})$. Most important, the difference between $\overline{f(C)}$ and $f(\overline{C})$ depends on the degree of the convexity. Thus, when species differ in their adult death rates, their growth rates (5) will differ in convexity. This outcome means that their time average growth rates (the $\overline{r_j}$) will be affected to different degrees by fluctuations in $C(t)$. In particular, a species with a smaller value of δ, which means a larger degree of convexity, has more to gain from fluctuations in $C(t)$.

The potential for Jensen's inequality to affect the species differentially is critical to the coexistence mechanism, relative nonlinearity, but alone it is not sufficient. To state the full sufficient conditions, note that the difference between $\overline{f(C)}$ and $f(\overline{C})$ depends not just on the convexity of f, but also on the variance of C. As the variance of C increases, the difference between $\overline{f(C)}$ and $f(\overline{C})$ increases. This increase is greater for a species with a smaller value of δ. Thus, large fluctuations in C give a relative advantage to a species with a small adult death rate, δ, in comparison to a species with a large adult death rate. Conversely, small fluctuations in C advantage a species with a large adult

death rate relative to a species with a small adult death rate. These differences in the effects of fluctuations on the species are important for species coexistence when the species also strongly influence the magnitude of fluctuations in C, as is possible in the lottery model. Most, important, it is possible for a species to cause levels of fluctuation in C that favor its competitors. This fact is clear from Eq. (4) which shows that the components of $\boldsymbol{\beta}$ are weighted by species densities in determining C. Thus, a species having a highly variable β (equivalently, a highly variable environmental response, E) will lead to high variation in C whenever it is abundant, regardless of its adult death rate. Hence, a species with a large value of δ and a highly variable β will, whenever it is abundant, favor a competitor with a small value of δ. In this way (and in others to be discussed below) species with different values of δ can individually promote conditions that are disadvantageous to themselves but favor their competitors, promoting coexistence by the mechanism relative nonlinearity.

As emphasized above, relative nonlinearity is not the only coexistence mechanism arising in the lottery model. The storage effect arises too. The storage effect depends on the fact that the growth rate $r_j(t)$, as best appreciated in the generic form (5), depends on the environmental response $E_j(t)$ interactively with $C(t)$, because $\partial r_j / \partial E_j \partial C$ is not zero. This interactive effect, as we shall see, can be separated from the nonlinear effect of $C(t)$ on $r_j(t)$ to reveal the storage effect as a distinct mechanism. The storage effect formalizes the concept of temporal niche partitioning. Because it has been much discussed elsewhere (Chesson and Warner 1981, Chesson 1994, Chesson 2003), we will only provide a brief introduction here.

One key component of storage effect is *covariance between environment and competition*. This covariance measures how much the ability of a species to benefit from favorable environmental conditions is inhibited by competition. It is measured for each species separately. High (positive) covariance means that benefits to a species from favorable environmental conditions are countered by increased competition at those times. In the lottery and similar models, such effects occur when a species is at high density because its strong responses to the physical environment place high demands on resources, as embodied in Eq. (4). However, low covariance means that the competition a species experiences is decoupled from its environmental response. Such decoupling becomes possible when a species is at low density. It means that the species has times when the environment is favorable, but competition is weak, allowing the species to take full advantage of those environmentally favorable times. In the lottery model, this means that strong recruitment occurs. Low covariance, however, also leads to times the environment is poor and competition is strong, leading to especially poor recruitment.

The storage effect, however, has another key component, which is manifested here as a persistent adult stage. The adult stage buffers a population against times when recruitment is poor. This means that strong recruitment gains during favorable times are not canceled out by population decline during unfavorable times. Mathematically, this effect is measured by the interaction between environment and competition, $\partial r_j / \partial E_j \partial C$, with a negative value implying buffered population growth, allowing low covariance between environment and competition to be a net advantage. As such low covariance is more likely at low than high density, recovery from low density is promoted, leading to the storage effect coexistence mechanism.

In most cases in nature, it can be expected that relatively nonlinear competition and an interaction between environmental responses and competition are both present. Thus, relative nonlinearity and the storage effect are expected often to be found together, as they are in the lottery model whenever adult death rates differ.

Quantifying coexistence: long-term growth rate and invasion analysis

In order to compare the contributions of relative nonlinearity and the storage effect to coexistence, we need a method to define their magnitudes. The invasibility criterion for species coexistence provides the needed quantification (Turelli 1981, Chesson 1994). The invasibility criterion uses the rate at which a species recovers from low density in the presence of its competitors to define the robustness of a species' persistence in the community. This recovery rate, which we denote as $\bar{r}_i$, can be partitioned into contributions to species persistence from different coexistence mechanisms, most notably, relative nonlinearity and the storage effect (Chesson 1994, Chesson 2003). Overall contributions of these mechanisms to coexistence in the community are derived by appropriately averaging their contributions to persistence of species individually, as discussed below under the section "community average coexistence mechanisms."

To evaluate the invasibility criterion, each species i is set in turn to zero density and its recovery rate, $\bar{r}_i$, is calculated as the expected change in ln population size per unit time, with the competitors of species i at the stationary distribution of population fluctuations that they have in its absence (Chesson 1994). The invasibility criterion

defines stable coexistence as positive recovery rates for all species. It has now been show

for fairly general circumstances that the invasibility criterion implies that the dynamics of

the species converge on a stationary stochastic process with all species at positive

densities (Schreiber et al. 2011). Diffusion approximations to the stationary distribution

for the lottery model have been worked out in the two species case (Hatfield and Chesson

1989) and for a class of multispecies cases (Hatfield and Chesson 1997).

The recovery $\overline{r}_i$ can be analyzed by approximating the growth rate $r_j(t)$ given by

Eq. (5) in terms of a quadratic function of the environmental response, $E_j(t)$, and the

competitive response, $C(t)$. Averaging over time, and comparing resident and invader

average growth rates, then allows the recovery rate to be partitioned into meaningful

components (Chesson 1994, Chesson 2003, 2008). The particular formulae for the

components needed here are derived in appendix I. The results are most simply expressed

when the recovery rate $\overline{r}_i$ is measured on the time scale of a generation, which is here $1/\delta_i$.

In these units, $\overline{r}_i$ takes the general form

$$\overline{r}_i \approx \eta_i - \overline{\eta}_s^{\{s \neq i\}} + \Psi_i. \tag{6}$$

The first term $\eta_i - \overline{\eta}_s^{\{s \neq i\}}$ is a comparison of the average fitness of the invader species i (η_i

, defined in table I) relative to the residents ($\overline{\eta}_s^{\{s \neq i\}}$) where the special notation $\overline{\eta}_s^{\{s \neq i\}}$

means the average over the set of species s not including species i. The quantity η is

found as the expected growth of a species from low density, on the generation time-scale,

with competition fixed–for details see Appendix I. In the absence of environmental

variation, the fitnesses, η_i, reduce to the quantities $\ln\left(\beta_j / \delta_j\right)$, which have the important

property that they predict which species will dominate in competition under those

circumstances. The quantity Ψ_i is only present when the environment varies, and consists

of the combined magnitudes of the coexistence mechanisms that can be present under

those circumstances.

In the absence of the coexistence mechanisms, the invasion rate is simply the

fitness comparison $\eta_i - \overline{\eta}_s^{\{s \neq i\}}$, and as a consequence, species with below average fitness

cannot invade. In the presence of coexistence mechanisms, a species with a negative

value of $\eta_i - \overline{\eta}_s^{\{s \neq i\}}$ can invade if

$$\eta_i - \overline{\eta}_s^{\{s \neq i\}} > -\Psi_i \tag{7}$$

Thus, the larger Ψ_i is, the larger the fitness disadvantage species *i* can suffer and still

invade. In the lottery model, Ψ_i has contributions from both relative nonlinearity (ΔN_i)

and the storage effect (ΔI_i):

$$\Psi_i = \Delta I_i - \Delta N_i , \tag{8}$$

given by the formulae in Table 1. Note that for historical reasons associated with its

derivation (Chesson 1994), relative nonlinearity is entered with a negative sign, and

therefore a negative value of ΔN_i promotes recovery of species *i*.

Relative nonlinearity depends multiplicatively on the variance in competition and

the difference in adult death rates (Table 1). In models with a single competitive factor,

such as *C* of the lottery model, ΔN_i has different signs for different species. As shown in

the formulae for relative nonlinearity in Table 1, ΔN_i will always be negative for species

with larger adult death rates, and positive for species with smaller adult death rates. To

promote stable coexistence, the mechanism must add more to the recovery rate of some

species than it subtracts from others—this gives the mechanism a positive contribution at

the community level, as discussed below. Coexistence by the storage effect is more

straightforward as its measure, ΔI_i, is often positive for all species, although we shall see important cases here when it is not. The species level mechanism measures ΔN_i and ΔI_i are best used for understanding persistence of an individual species in competition with others. To gain an overall understanding of how coexistence is promoted in the community, we need to use community average measures, which we discuss next.

Community average coexistence mechanisms

In the community average approach, the overall tendency for recovery from low density is assessed by averaging the invader growth rates (6) over species. In this process, it is important to appreciate that growth rates are in expressed in per generation units, as discussed above, which are the most meaningful units for making species comparisons (Chesson 2003, 2008). Taking this average in (6), we obtain

$$\frac{1}{n}\sum_{i=1}^{n} \overline{r_i} = \overline{\Psi} , \qquad (9)$$

i.e. just the average of the Ψ_i because the fitness comparisons, $\eta_i - \overline{\eta}_s^{\{s \neq i\}}$, necessarily average to zero. In terms of (9), we can regard the mechanisms as promoting coexistence on average if

$$\overline{\Psi} = \overline{\Delta I} - \overline{\Delta N} \qquad (10)$$

is larger than 0. The individual invasion rates can then be written in terms of the community average as

$$\overline{r_i} = \xi_i + \overline{\Psi} , \qquad (11)$$

where ξ_i is a modification of the fitness-difference $\eta_i - \overline{\eta}_s^{\{s\neq i\}}$ accounting for the

asymmetries in the actions of the coexistence mechanisms, and thus takes the form

$$\begin{aligned}\xi_i &= \eta_i - \overline{\eta}_s^{\{s\neq i\}} + \left(\Delta I_i - \overline{\Delta I}\right) - \left(\Delta N_i - \overline{\Delta N}\right)\\ &= \eta_i - \overline{\eta}_s^{\{s\neq i\}} + \delta I_i - \delta N_i\end{aligned} \tag{12}$$

Here, the deviations of the species level mechanisms from their community averages are

denoted δI_i and δN_i. In most models, and the lottery model is no exception, η is defined

in terms of more basic model parameters. In the lottery model a natural parameter is

μ. This parameter has the desirable property that it is exactly equal to η in the absence of

environmental variation and predicts the dominant species. With environmental variation,

$$\eta_j \approx \mu_j + \tfrac{1}{2}\left(1-\delta_j\right)\sigma_j^2. \tag{13}$$

This means that the fitness comparison in the absence of the mechanism is written in

terms of μ differences, plus a term δV_i involving variances and adult death rates (Table 1).

Table 1

	Species Level	Community Level
Average Fitness Difference	$\eta_i - \overline{\eta}_s^{\{s\neq i\}} = \delta\mu_i + \delta V_i$	n.a.
Relative Nonlinearity	$\dfrac{1}{2}V(C^{\{-i\}})(\delta_i - \overline{\delta}_s^{\{s\neq i\}})$	$-\dfrac{n}{2}\operatorname{cov}_i\left(\overline{\delta}_s^{\{s\neq i\}}, V(C^{\{-i\}})\right)$
Storage Effect	$\overline{(1-\delta_s)\chi_s^{\{-i\}}}^{\{s\neq i\}} - (1-\delta_i)\chi_i^{\{-i\}}$	$\overline{\overline{(1-\delta_s)\chi_s^{\{-i\}}}^{\{s\neq i\}} - (1-\delta_s)\chi_s^{\{-s\}}}^s$

Notes: The variable μ_j is the mean ln life-time fecundity for species j and is defined as $\mu_j = E[E_j] - \ln\delta_j$, and $E[]$ means expected value. The mean ln life-time fecundity comparison between species is defined as $\delta\mu_i = \mu_i - \overline{\mu}_s^{\{s\neq i\}}$. The variable σ_j^2 is the variance of the environmental response for species j: $\sigma_j^2 = V\left(E_j\right)$. δV_i is the contribution from variance differences in ln fecundity between species to average fitness differences $\delta V_i = \tfrac{1}{2}\left(1-\delta_i\right)\sigma_i^2 - \overline{\tfrac{1}{2}\left(1-\delta_s\right)\sigma_s^2}^{\{s\neq i\}}$. The variable $C^{(-i)}$ is the competitive response of all species in the community when species i is the invader, and $\chi_j^{(-i)} = \operatorname{cov}(E_j, C^{(-i)})$ is the covariance between environment and competition for species j when i is the invader. Measurements of the coexistence mechanism are in the natural scale of a generation.

The community average measures, $\overline{\Delta I}$ and $\overline{\Delta N}$, define the overall roles of the mechanisms in stabilizing coexistence. The stronger these community average measures are, the more fitness inequality can be tolerated compatible with coexistence. These community average measures are the stabilizing components of the mechanisms (Chesson 2000, 2003) because they are necessary for stable coexistence, and lead to it if they are large enough. Moreover, to a large extent, stabilizing components determine the size of the coexistence region measured in terms of average fitness differences. For instance from Eq. (11), we see that the species coexist if

$$\min_i \xi_i > -\overline{\Psi} \,. \tag{14}$$

Hence, if the ξ can be varied independently of $\overline{\Psi}$ then we see that $\overline{\Psi}$ determines the size of the coexistence region in terms of the average fitness inequalities, ξ. A larger value of $\overline{\Psi}$ gives a larger region of ξ values permitting coexistence. We shall see later that the ξ values can be varied by varying the μ values given by Eq. (13) in the two species case with no effect on $\overline{\Psi}$. Beyond the two species coexistence $\overline{\Psi}$ does depend on the μ values too, but the effects are relatively small, and so the magnitude of the coexistence region is still largely determined by $\overline{\Psi}$. By looking at the major factors affecting $\overline{\Psi}$ we can come to an understanding the major factors affecting species coexistence.

Given $\overline{\Psi}$, the ability of any individual species to coexist with the others depends on its particular ξ value, which in turn depends on the deviations δI_i and δN_i of the mechanisms from the community average (Eq. 12). These terms are said to be equalizing (Chesson 2000, 2003) if they reduce fitness inequality. Note, however, that δI_i and δN_i might increase rather than decrease fitness inequality depending on their signs and magnitudes relative to the average fitness comparisons, $\eta_i - \overline{\eta}_s^{\{s \neq i\}}$, in their absence.

Separate consideration of stabilizing and equalizing components of the storage effect and relative nonlinearity are critical because relative nonlinearity always acts unequally on the various species in a community whenever it is present, and the storage effect will commonly act somewhat unequally on the different species (Chesson 2003).

The community average measures have instructive general formulae (Chesson 2003, 2008). Community average relative nonlinearity, $\overline{\Delta N}$, takes the form of a covariance (appendix I) :

$$\overline{\Delta N} = -\frac{n}{2} \operatorname{cov}_i \left(\overline{\delta}_s^{\{s \neq i\}}, V(C^{\{-i\}}) \right).$$
(15)

It is a covariance between the variance in competition that residents generate $V(C^{\{-i\}})$ and the average death rate $\overline{\delta}_s^{\{s \neq i\}}$ of the resident species. The covariance is taken over different possible sets of resident species, indexed by the invader i, which defines which of the n species in question is missing from the resident set. Note that this mechanism magnitude is a direct measure of the association between the nonlinearities of species' growth rate and the variance in competition that they generate as residents. Because $\overline{\Delta N}$ contributes to the long term growth rate with a negative sign, as shown in Eq. 10, positive covariance between the adult death rate and variance in competition leads to a stabilizing effect. Thus this formula embodies quantitatively the understanding given above that for relative nonlinearity to stabilize coexistence, species with larger death rates must generate larger variation in competitive factors when they are resident species.

The community average storage effect is similarly a precise mathematical expression of the understanding the mechanism. It is given as a comparison of resident and invader state covariances between environment and competition, which are then

weighted by the adult survival rate (specifying the degree of buffering of population growth) and averaged over species as follows:

$$\overline{\Delta I} = \frac{1}{n}\sum_{j=1}^{n}(1-\delta_j)\left(\overline{\chi_j^{\{-i\}}}^{\{i\neq j\}} - \chi_j^{\{-j\}} \right) \; . \tag{16}$$

Here, the critical comparisons of covariance between environment and competition are within species: The covariance, $\chi_j^{\{-j\}}$, of species j in the invader state is compared with its average covariance, $\overline{\chi_j^{\{-i\}}}^{\{i\neq j\}}$, in the resident state, for each other species i in the invader state. If species, on weighted average, have higher resident-state covariance than invader-state covariance, the community average storage effect is positive, and therefore stabilizing.

Our focus in this study is on comparing the community average storage effect and community average relative nonlinearity as these provide the necessary requirements for stable coexistence and determine the size of the coexistence region in terms of average fitness differences (ξ_i, Eq. 12) compatible with coexistence. In the work that follows, we are concerned both with features that make relative nonlinearity large and that make the storage effect small.

Cases to be considered

In each of the cases studied below, we looked at mechanisms measured in both two-species and multispecies cases. Though multispecies measures share many properties with their two-species counterparts, the behavior of coexistence mechanisms as the number of species increases can be informative. In some situations there are qualitative

differences between two-species and multispecies cases. These differences arise because in a two-species community there is only one resident species. This single resident species fills the fixed amount of space in the system, and so it stays at a fixed adult density. Fluctuations in competitive factor then reflect the fluctuations in environmental response of the resident species alone. Indeed, the response to competition is equal to the response to the environment of the resident species in this case. When there are multiple resident species interacting with each other, more factors come into play to affect the fluctuations in competition. Factors that affect the strength of relative nonlinearity in the multispecies case but not in the two-species case include the correlations between the environmental responses of different species, and differences between species in mean fecundity. Other factors such as adult death rate differences, and differences between species in their sensitivity to the environment, should matter regardless of the number of species. With these considerations, we lay out the critical cases to be studied.

Case (1) *Adult death rate differences*.

Adult death rate differences have two distinct effects on the magnitude of relative nonlinearity as a coexistence mechanism. First, the difference in the curvature of the growth rates (the relative nonlinearity of the growth rates) of any two species is equal to their difference in adult death rate. Second, with multiple resident species, residents with higher adult death rates generate larger fluctuations in competition than residents with low adult death rates. This occurs because species with higher adult death rates have higher population turnover and so their populations fluctuate more, in turn causing higher fluctuations in competition. Higher population turnover carries over to larger fluctuations

in competition (Chesson 2000). Therefore, relative nonlinearity is expected to increase with differences in adult death rates. In the two-species case, however, there is only one resident species, and its population density does not vary. In that case, there is no effect of resident adult death rate on the variance in competition. Only the effects on the relative nonlinearities of the growth rates matter in this case.

Case (2) *Differences between species in sensitivity to the environment.*

In the lottery and similar models of competition in a variable environment, the physical environment is not modeled directly, but the environmental response is assumed to reflect the species' response to underlying physical environmental variables. Thus, the variance in a species' environmental response can be assumed to reflect the species' sensitivity to the underlying physical environmental variables. Most important for our considerations here, a more sensitive species generates more fluctuation in competition as a resident. Fluctuation differences generated in this way are likely to be much stronger than those generated by longevity differences because C is directly a function of each species' environmental response (Eq. 4). If a more sensitive species also has a higher adult death rate, relative nonlinearity will increase with the differences in sensitivities.

Case (3) *Synchrony between species in environmental response.*

Competition is likely to fluctuate more as resident species become more synchronized (more correlated) in their environmental responses because then their separate contributions to competition through their environmental responses will reinforce one another, leading to greater fluctuations in the total demand for space

included in Eq. (4) for *C*. Synchrony should also have a large negative effect on the storage effect because in past work the storage effect has been shown to decrease linearly with the correlations of the environmental responses (Chesson 2003). Thus, synchrony between species is predicted to have a large effect on the relative magnitude of relative nonlinearity compared with the storage effect.

Case (4) *Mean fitness differences*.

The mean fitnesses η are equal to ln mean life-time reproduction ("mean fecundity") when the environment is constant, and have a strong effect on the relative abundance of a resident species (Chesson 2003), although the relationship depends greatly also on other parameters. With multiple resident species, a species with much larger mean fecundity than the other species is likely to dominate resident species densities, which means that competition will mostly reflect this species. The effect on relative nonlinearity is not straightforward to predict, but does need to be understood because if the effects are strong, then the effects of mean fitness differences and mechanism magnitudes on species coexistence are not independent, complicating the interpretation of the invasion condition (Eq. 7). To simplify the analysis, we focus on one especially valuable scenario: how the mechanisms change as the mean fecundity of one species is moved towards its invasion boundary. To do this, we decrease the mean fecundity of each species in turn until its invasion rate is zero and study the changes in the mechanisms over this gradient. We only study cases when relative nonlinearity has a stabilizing effect, i.e. when shorter-lived species are more sensitive to the environment.

Except for case (4) where the two-species analysis is not needed, we study each case above for both two-species and three-species communities. Analytical approximations of sufficient accuracy are available for the two-species lottery model, but in the three species case we use simulations to derive the resident competition variance. Studies of two species communities dominate the theoretical literature on competition, but such studies are inadequate when the efficacy of a mechanism can depend greatly on the number of species. As relative nonlinearity has been predicted to be ineffective in promoting coexistence beyond the two species case, it is critical that we study it for the multispecies situation as well. However, because these simulations are stochastic, high replication is needed and this need increases dramatically with the number of species. For this reason, we do not go beyond the three species case.

RESULTS

Community average level

In our investigation, we kept the average variance in the environmental response fixed, and varied only the relative variances (σ_1 / σ_2) for the different species. In the two species case, the storage effect and relative nonlinearity are linear functions of variances and covariances (Table 2), and so the relative magnitudes of these mechanisms depend on the relative magnitudes of the variances, not their absolute values. In the three species case, our simulations showed negligible effects of the absolute values of the variances, σ_j^2, on relative mechanism magnitude if species averages of these variances are 0.5 or less, and no individual variance is greater than 1 (spp Fig 1.). With fixed relative variances, the

absolute magnitudes of the storage effect and relative nonlinearity are approximately

proportional to the average variance, which is fixed at 0.5 in the remainder of this study.

Table 2 two species case

Mechanism	Species Level	Community Level
Relative Nonlinearity	$\frac{1}{2}(\delta_i - \delta_r)\sigma_r^2$	$\frac{1}{4}(\delta_1 - \delta_2)(\sigma_2^2 - \sigma_1^2)$
Storage Effect	$-(1-\delta_i)\sigma_{ir} + (1-\delta_r)\sigma_r^2$	$\frac{1}{2}((\sigma_1^2 - \sigma_{12})(1-\delta_1) + (\sigma_2^2 - \sigma_{21})(1-\delta_2))$

Legend δ_j: adult death rate for species j; σ_j^2: variance in environmental response for species j; σ_{ir}: covariance between the environmental responses of species i and species r, $\sigma_{ir} = \rho_{ir}\sigma_i\sigma_r$ with ρ_{ir} the correlation between environmental responses.

The effect of adult death rate differences alone

The strength of relative nonlinearity increases with the differences in death rates

as expected (Fig 1). However, these death rate differences alone lead to only small

differences in the variance of competition. Thus, when there are no differences in

species' sensitivities to environmental fluctuations, relative nonlinearity is small in

magnitude compared with the storage effect (Fig. 1a). In the case of equal sensitivity,

both the storage effect and relative nonlinearity increase slightly with differences in death

rate, but relative nonlinearity increases slightly faster in relative magnitude. Thus,

although small, the proportional contribution of relative nonlinearity to stabilizing

coexistence increases slightly with adult death rate differences (Fig. 2b middle curve).

Because these effects on relative nonlinearity depend on fluctuations in resident densities,

they are not found in the two-species case with species equally sensitive to

environmental fluctuations, as the single-species resident does not fluctuate in density

and the community average relative nonlinearity is zero ($\sigma_1^2 - \sigma_2^2 = 0$ in table 2)
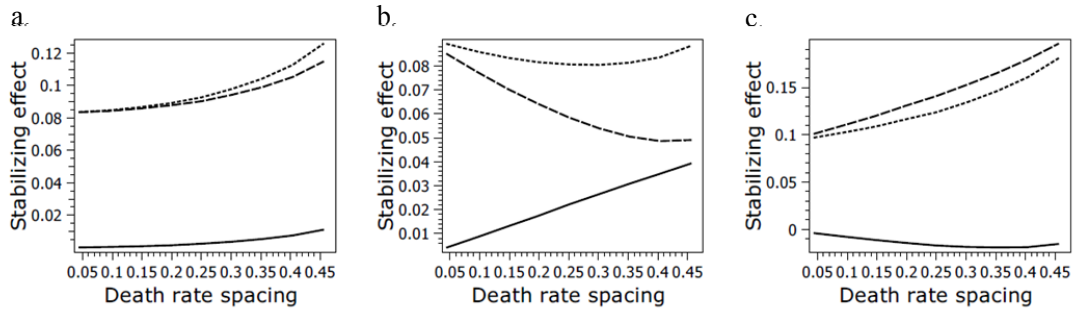
Figure 1. In (a), (b), and (c) the stabilizing effects of relative nonlinearity ($-\overline{\Delta N}$, solid line), the storage effect ($\overline{\Delta I}$, dashed line), and the overall stabilizing effect ($-\overline{\Delta N} + \overline{\Delta I}$, dotted line) are plotted against death rate spacing. The three panels area are: species have common sensitivities to environmental fluctuations (a), shorter-lived species more sensitive (b), and longer-lived species more sensitive (c). *Parameters*: $\mu_1 = \mu_2 = \mu_3$; $\rho = 1/3$; $\overline{\delta} = 0.5$, with δ_1 and δ_3 spaced equally about the mean; $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1{:}6{:}11$ for (b) or $= 11{:}6{:}1$ for (c).

The effect of differences in sensitivity to the environment

Adult death rate differences are essential for relative nonlinearity, but the magnitude of relative nonlinearity is much greater when species differ also in their sensitivities to the environment (Fig. 1b&c). The magnitude of relative nonlinearity increases rapidly with species differences in sensitivity to the environment, because these sensitivity differences cause the variance of competition to vary greatly with the identities of the resident species. Sensitivity differences cause much bigger differences in the variance of competition than adult death rate differences. Indeed, the critical covariance between adult death rates and variance in competition (Eq. 13) can be positive when longer-lived species are more sensitive to the environment, a situation that does not arise with adult death rate differences alone. Moreover, in this case, relative nonlinearity is a destabilizing mechanism, promoting competitive exclusion rather than coexistence (Fig. 1c, Fig. 2 dotted lines). This effect is not monotonic in the adult death differences, but

achieves a maximum for an intermediate spacing in these figures. However, with the

opposite relationship between environmental sensitivity and adult death rates, i.e. when

shorter-lived species are more sensitive to the environment, relative nonlinearity can have

a strong stabilizing effect on species coexistence, an effect that increases monotonically

as adult death rate differences increase (Fig. 1b, Fig. 2 dashed lines).
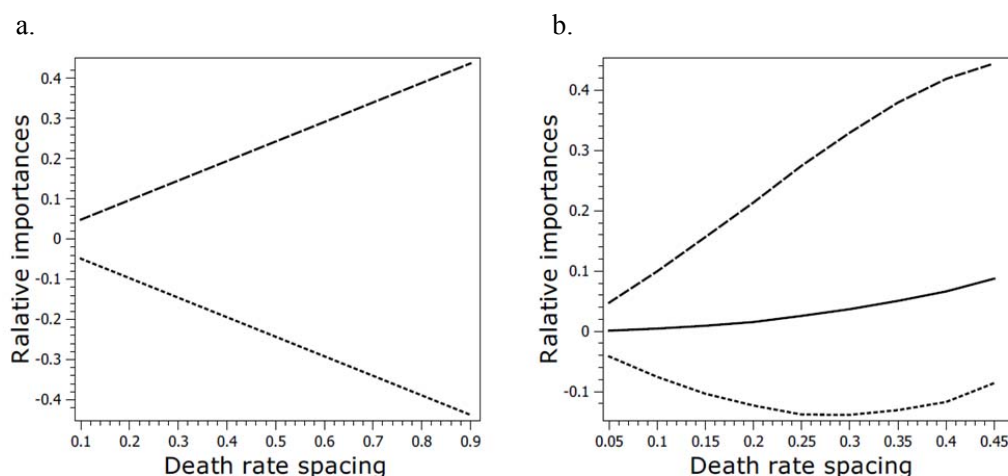

Figure 2. The relative contribution of relative nonlinearity to the overall stabilizing effect ($-\overline{\Delta N} / (-\overline{\Delta N} + \overline{\Delta I})$) as a function of death rate spacing in two species (a) and three species cases (b). In each panel, comparisons are made between the case where shorter-lived species are more sensitive to the environment (dashed line) and the case where longer-lived species are more sensitive (dotted line). The case of equal sensitivities to environmental fluctuations (solid line) applies only to the three species case (b). *Parameters*: $\mu_1 = \mu_2 = \mu_3, \rho = \frac{1}{3}$; in (a) $\sigma_1^2 : \sigma_2^2 = 1 : 2$ (dashed line) or 2:1 (dotted line); in (b) $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = $ 1:6:11 (dashed line) or 11:6:1 (dotted line).

The storage effect shows the opposite trend to relative nonlinearity: it decreases

with death rate differences when shorter-lived species are more sensitive to the

environment (Fig. 1b), and increases with death rate differences when shorter-lived

species are less sensitive to the environment (Fig. 1c). Because of this opposite behavior

of the storage effect and relative nonlinearity, relative nonlinearity adds more as a

proportion to stability when shorter-lived species are more sensitive than it subtracts

when shorter-lived species are less sensitive. However, in both cases, the storage effect largely compensates for changes in relative nonlinearity (Fig. 1b) or drives the overall stabilizing effect because it is much larger than relative nonlinearity (Fig. 1c).

The effect of synchrony between species in environmental responses.

In the two species case, the degree of correlation in environmental responses between species has no effect on the absolute magnitude of relative nonlinearity as it does not affect resident competition. In the three species case, increasing correlation can have opposite effects on the absolute magnitude of relative nonlinearity depending on whether species have different sensitivities to the environment. When species are equally sensitive to the environment, increasing correlation further reduces the weak relative nonlinearity (Fig. 3a). When the sensitivities differ, increasing correlation increases the magnitude of the relative nonlinearity: it either leads to a stronger stabilizing effect of relative nonlinearity if shorter-lived species are more sensitive (Fig. 3b) or a stronger destabilizing effect if longer-lived species are more sensitive (Fig. 3c).

The storage effect always declines linearly as the correlation increases (Fig. 3). The effect of correlation on the storage effect is stronger than on the relative nonlinearity. Thus, the relative magnitude of relative nonlinearity always increases with correlation, in large part due to the rapid decline of the storage effect (Fig. 4). When the shorter-lived species is more sensitive to environment, the storage effect can be weaker than the relative nonlinearity as correlation increases (Fig.3b, 4). It happens in two species cases that the storage effect goes negative as the correlation goes above certain level (Fig. 4a). In this situation, relative nonlinearity can be solely responsible for species coexistence.
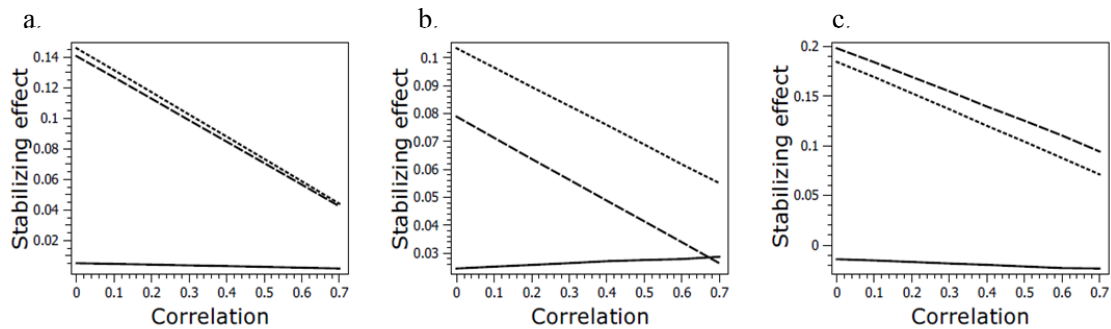
Figure 3. In (a), (b), (c) stabilizing effect of relative nonlinearity (solid line), the storage effect (dashed line), and the overall stabilizing effect (dotted line) are plotted against increasing correlation in environmental responses. Comparisons are made between three situations: species have the same sensitivity (a), shorter-lived species are more sensitive (b) and longer-lived species are more sensitive (c). *Parameters*: $\mu_1 = \mu_2 = \mu_3$, $\delta_1 = 0.2, \delta_2 = 0.5, \delta_3 = 0.8$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 =$ 1:6:11 for (b) or , 11:6:1 for (c).
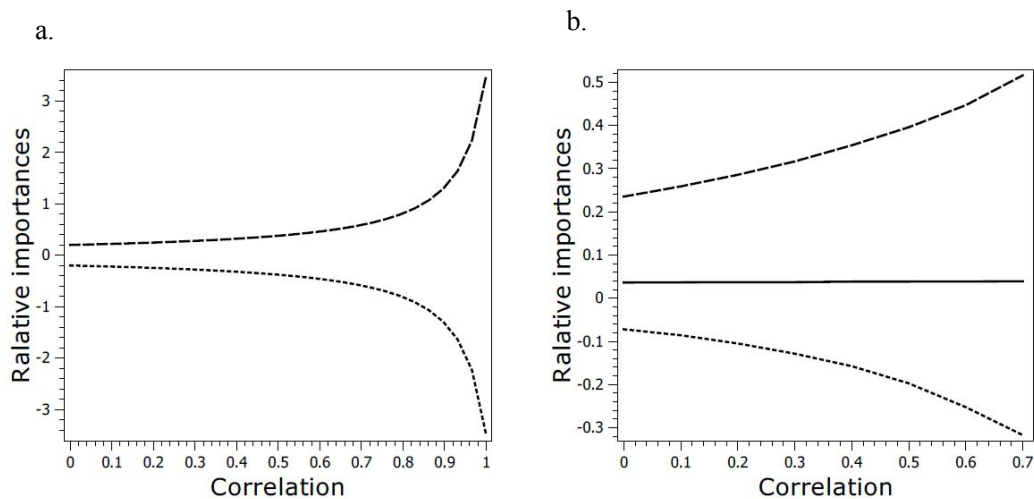

Figure 4. The relative contribution of relative nonlinearity to the overall stabilizing effect ($-\overline{\Delta N} / (-\overline{\Delta N} + \overline{\Delta I})$) as a function of correlation between environmental responses. Dashed line: shorter-lived species more sensitive. Dotted lines, longer-lived species more sensitive; Solid lines, species equally sensitive to the environment. *Parameters*: $\mu_1 = \mu_2 = \mu_3$; (a) $(\delta_1, \delta_2) = (0.2,$

0.8), $\sigma_1^2 : \sigma_2^2 = 1:2$ (dashed line) or 2:1 (dotted line); (b) $(\delta_1, \delta_2, \delta_3) = (0.2, 0.5, 0.8)$ $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 =$ 1:6:11 (dashed line) or 11:6:1 (dotted line).

The effect of mean fitness differences

      Although all previous scenarios are investigated with species having equal mean ln life-time fecundity (equal μ values), the conclusions are robust to such μ differences. First note that in the two-species case, relative nonlinearity and the storage effect are both independent of μ differences, which is the ideal condition for the stabilizing effect $\overline{\Psi}$ to be a direct measure of coexistence region in terms of range of ξ values that allows species to coexistence (Eq. 14). In three species cases, the overall stabilizing effect will change with μ differences; the direction of the changes depends on which species in the community is in disadvantage (Table 3). Nevertheless, the subtle difference in the overall stabilizing effect between invasion boundary and the interior of coexistence region is too small to change our conclusions based on the case of equal μ values (Table 3). This result is reassuringthat in the three species case, the overall stabilizing effect is a satisfactory measure of the coexistence region given the minimal impact of μ differences on the stabilizing effect.

      The small effects of μ differences on the overall stabilizing effect is partially due to the opposite responses of relative nonlinearity and the storage effect as μ differences vary (Supp. Fig. 2). Both mechanisms change essentially linearly with μ differences: when μ of either the least sensitive species (also the longest-lived species) or the most sensitive species (also the shortest-lived species) is reduced, relative nonlinearity is reduced and the storage effect is increased (Supp. Fig. 2 a&c); the opposite is found when the μ of the median sensitive species (also the species with median longevity) is reduced

(Supp. Fig. 2b). Nevertheless, the effects of μ differences on the community average

storage effect and relative nonlinearity are still small, as we can tell from the slopes of the

lines in Supp Fig. 2.

Table 3. Sensitivities of coexistence mechanisms to mean ln life time fecundity

Correlation ρ	Species i	$\dfrac{\partial(\delta I_i - \delta N_i)}{\partial \mu_i}$	$\dfrac{\partial(\overline{\Delta I} - \overline{\Delta N})}{\partial \mu_i}$	$\partial \mu_i$
$\rho = 0$	$i = 1$	-0.032	0.031	-0.112
	$i = 2$	0.013	-0.013	-0.088
	$i = 3$	-0.046	0.046	-0.048
$\rho = 0.3$	$i = 1$	-0.024	0.023	-0.102
	$i = 2$	0.038	-0.038	-0.061
	$i = 3$	-0.037	0.037	-0.035
$\rho = 0.6$	$i = 1$	-0.104	0.108	-0.093
	$i = 2$	0.143	-0.144	-0.033
	$i = 3$	-0.148	0.054	-0.023

Notes: The quantity δI_i and δN_i are deviations of the species-level storage effect and the species-level relative nonlinearity for species i from the community averages: $\delta I_i = \Delta I_i - \overline{\Delta I}$ and $\delta N_i = \Delta N_i - \overline{\Delta N}$. Columns 3 and 4 are average slopes of $\delta I_i - \delta N_i$ and $\overline{\Delta I} - \overline{\Delta N}$ as μ_i varies from the invasion boundary to interior of coexistence regions (equal μ values), and the change in μ_i is given by $\partial \mu_i$ in the last column. Different level of correlation in environmental responses between species is listed in column 1 and the species whose μ gets varied is listed in column 2, and. *Parameters*: $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1{:}6{:}11$.

Mechanism asymmetries and coexistence regions

So far we have focused simply on the community average components of the

coexistence mechanisms, but in general both mechanisms make unequal contributions to

the recovery rates of different species. These unequal contributions can be examined

through the mean fitness adjustment, δI_i and δN_i. In the two species case, these mean

fitness adjustments are available analytically, and the fitness comparison ξ, reduces to the

following form

$$\xi_i = \delta\mu_i + \underbrace{\tfrac{1}{2}(\delta_i - \delta_r)\sigma_{ir}}_{\delta V_i + \delta I_i} - \underbrace{\tfrac{1}{2}(\delta_i - \delta_r)\overline{\sigma^2}}_{\delta N_i} . \tag{17}$$

(Appendix II), where σ_{ir} is the covariance between E_i and E_r, and $\overline{\sigma^2}$ is the average of the variances in the environmental responses (E) across species. Relative nonlinearity is only present when the δ's of the two species are different. Of necessity δN_i is non-zero. If δN_i has the same sign as the combination $\delta\mu_i + \delta V_i + \delta I_i$ it will have the net effect of promoting coexistence. Moreover, as δN_i is always larger in magnitude than $\overline{\Delta N}$, the fitness equalizing effect of relative nonlinearity is likely often to be more important than its stabilizing effect (Supp. Fig. 3). However, as μ can be changed independently of the mechanisms, these fitness comparison components do not affect the size of the coexistence region in terms of the range of μ values compatible with coexistence. With three species, there is some sensitivity of the mechanism to μ but the sensitivity is low (Table 3), and so for general considerations of the extent to which these mechanisms promote coexistence, focus on community average measures is sufficient. However, this result likely does not generalize to models where relative nonlinearity is present alone because in those cases, up to quadratic level of approximation, the strong asymmetries between species with relative nonlinearity preclude the coexistence of more than two species (Chesson 1994).

Discussion

The lottery model, which we investigate here, is a common model for understanding the role of recruitment variation in species coexistence in nature. Whereas

previous studies have focused almost exclusively on the storage effect, our work identifies situations in which relative nonlinearity can have an important role too. We find that in the lottery model, relative nonlinearity can be important in the stabilization of species coexistence, both absolutely, and in comparison to the storage effect. Relative nonlinearity is present together with the storage effect whenever the adult death rates (equivalently the mean lifetimes) differ between species. The question is not whether relative nonlinearity should occur, but whether it is large enough to be important. We have found that it can be important in several different ways. It can have large effects on stabilization of fitness at the community level, which can be positive and thereby promote stable coexistence, or negative and thereby promote exclusion. It can also have large effects on fitness inequality, either equalizing fitnesses and promoting coexistence in that way, or it can lead to high fitness inequality and promote exclusion.

Stabilizing and destabilizing effects at the community level work through average rates of recovery across species, either increasing them and leading to higher stability or decreasing them and lowering stability. These changes can also be interpreted in terms of increases or decreases in the size of the parameter space compatible with coexistence. The effects on fitness inequality are seen from the species level mechanism measures. Relative nonlinearity always makes asymmetrical contributions to the recovery of different species from low density. This effect can promote coexistence of a set of species with given parameters if it tends to equalize average fitnesses between species, or promote exclusion if it creates larger average fitness differences between species.

The relative nonlinearity coexistence mechanism depends on per capita growth rates, here measured as $r_j(t) = \ln \lambda_i(t)$, to be relatively nonlinear functions of competition.

Adult death rate differences provide this key requirement in models like the lottery model of recruitment variation in discrete time, appropriate for seasonally reproducing species (Kuang and Chesson 2009), as explained above (*Relative nonlinearity and the storage effect in the lottery model*). Relatively nonlinear growth rates combine with the variance in competition to affect the rates of recovery of species from low density, and hence species coexistence. To get an overall stabilizing effect of relative nonlinearity, shorter-lived species should generate stronger fluctuations in competition when they are abundant, and reciprocally, longer-lived species should generate weaker fluctuations in competition. These conditions mean that shorter-lived species create the conditions that favor recovery of longer-lived species from low density and vice versa. These effects are explained here in terms of how Jensen's inequality gives a stronger boost to the long-term growth rate of longer-lived species than to shorter-lived species. The community average measure of the mechanism quantifies this effect in terms of the average across the community of the long-term rates of recovery from low density (the "invasion rates", $\bar{r}_i$). The community average measure of relative nonlinearity expresses the required relationship precisely as the covariance between the average adult death rates of resident species and the variance in competition that they generate (Table 1).

Larger resident adult death rates are naturally associated with higher variance in competition provided all species are equally sensitive to the environment. This occurs because variance in competition is jointly dependent on fluctuations in adult densities and direct contributions from fluctuations in the environmental response ($E = \ln \beta = \ln$ fecundity). Large resident adult deaths mean higher population turnover and hence greater population fluctuations in comparison with residents with smaller adult death

rates. This effect creates the required covariance between resident adult death rates and variance in competition for an overall stabilizing effect of relative nonlinearity at the community level (a negative value of $\overline{\Delta N}$). However, in this case of equal sensitivity to the environment (equal variances of species' environmental responses), relative nonlinearity is weak compared with the storage effect, which must be present too, and is therefore not an important promoter of coexistence. Moreover, relative nonlinearity cannot promote coexistence in the two-species case with equal environmental sensitivity because the single-species resident occupies all space and does not fluctuate in density, and so there is no contribution from density fluctuations in that case. Instead, fluctuations in competition from the single-species resident come only from the direct effects of fluctuations in the resident's environmental response. More generally, the direct effects of fluctuations in the environmental responses have much stronger effects on fluctuations in competition than do fluctuations in adult densities. It follows that differences in sensitivity of different species to the environment create much stronger differences between sets of resident species in the variance of competition than do differences in adult death rates. Consequently, a strong stabilizing effect of relative nonlinearity arises when shorter-lived species are more sensitive to the environment. Conversely, when longer-lived species are more sensitive to the environment, a strong destabilizing effect can occur at the community level (large positive value of $\overline{\Delta N}$).

Fluctuations in competition are intensified by positive correlations between species in their environmental responses. This has the effect of increasing the magnitude of relative nonlinearity ($\overline{\Delta N}$), but it has a negative effect on the magnitude of the storage effect ($\overline{\Delta I}$), and so this situation can make relative nonlinearity important in comparison

to the storage effect (Fig 4). This occurs whether relative nonlinearity has positive or negative effects on species coexistence. Moreover, in the two-species case, the community average storage effect ($\overline{\Delta I}$) can be negative when relative nonlinearity has a net stabilizing effect, meaning that the contributions of relative nonlinearity to coexistence overcome a strong destabilizing effect of the storage effect (Fig 4a, upper curve). In the multi-species case, we were not able to identify cases where relative nonlinearity makes a stronger contribution to coexistence than the storage effect, but nevertheless, its contributions can still be of comparable magnitude. In both the two-species and multispecies cases, community average relative nonlinearity is of comparable or stronger magnitude than the community average storage effect when shorter-lived species are more sensitive to the environment and there is a strong correlation between species in these sensitivities.

Our key results on the community average storage effect were determined for the case of equal mean ln life-time fecundity ($\mu = E\left[\ln \beta / \delta\right]$), which equalizes average fitnesses between species in the constant environment case. However, in the two-species case, the relative nonlinearity and storage effect measures are independent of the μ values. In the three-species case, these do change with μ, but since the sensitivity of these measures to μ in our studies is much less than 1, these community average measures, and the μ values, are relatively independent. Moreover, the species level contributions of the coexistence mechanisms are also relatively insensitive to μ. These facts mean that the community average measures are able to indicate the size of the coexistence region expressed in μ values. In the case where relative nonlinearity is expected to make the most important contributions to coexistence (shorter-lived species are more sensitive to

the environment) positive net stabilizing effects ($\overline{\Delta I} - \overline{\Delta N}$) do not guarantee coexistence in the multispecies case at equal μ values. As net stabilizing effects indicate only the average contribution of species to recovery from low density, this outcome is not surprising. However, using a measure of fluctuation stability (the average tendency of the coexisting species to remain away from zero density), we found that strong fluctuational stability could always be found for some μ values even though coexistence may not have been possible at equal μ values (Appendix IV).

Relative nonlinearity is an inherently asymmetric mechanism, and at the species level makes negative contributions (positive values of ΔN_i) for species with larger than average adult death rates, and positive contributions (negative values of ΔN_i) for other species. A net stabilizing effect results when the positive contributions outweigh the negative contributions in the average over species. Persistence of individual species with given parameters, however, can be helped or hindered by relative nonlinearity. Relative nonlinearity becomes an equalizing mechanism when it helps species with average fitness disadvantages, as measured by the μ values (ln mean life time fecundity in the absence of competition). Here that means the presence of tradeoffs between species where μ values are smaller for species with small adult death rates. Fecundity and longevity are predicted by life-history theory to indeed to tradeoff negatively between species (Charnov 1991, 1993, 1997), but here a greater proportional tradeoff is needed as fecundity is measured on adult life-time, i.e. average annual fecundity is multiplied by longevity.

A strong net stabilizing effect of relative nonlinearity at the community level requires a different sort of life-history tradeoff: shorter-lived species must be more sensitive to the environment. However, life-history theory as worked out in single-

species models, mostly predicts that species that are more sensitive to the environment should be longer-lived (Bulmer 1985, Real and Ellner 1992) in contradiction of the requirements for a strong stabilizing effect of relative nonlinearity. It would good to have life-history theory for multispecies contexts to be confident of the relevance of this prediction, but as it stands it implies that a strong destabilizing effect of relative nonlinearity is more likely in nature than a strong stabilizing effect. This means in the lottery model that coexistence would rely on a stronger storage effect to counteract the negative contribution of relative nonlinearity.

Many theoretical studies of coexistence focus on two species scenarios assuming that a generalization from the two species case is possible. However, we find fundamental differences between two species scenarios and multispecies scenarios. As mentioned, the differences arise because in two species cases there is only one resident species. The effects of correlation and mean fecundity difference on relative nonlinearity arise only with more than one resident species. This is because these two factors change competition fluctuations by their effects on the dynamics of resident species.

We find that relative nonlinearity is much larger and is able to contribute in a greater proportion to stable coexistence in the two species case than the three species case (Figs 2&4). As mentioned above, relative nonlinearity can maintain coexistence of more than two species only with difficulty when it is the only stabilizing mechanism (Chesson 1994). As relative nonlinearity relies on differences in the variance of competition between sets of resident species that differ only in which one of the n species in the community is missing from that set of resident species, it is likely to become weaker as n increases because such differences between different resident communities are

necessarily smaller. However, it is also known the storage effect will decrease in magnitude as diversity increases because there are fewer times when an individual species is favored more strongly by the environment than any other species. At present we do not know whether relative nonlinearity declines more strongly than the storage effect as diversity increases. Simple generalization from two species to many species is impossible for serious questions of diversity maintenance.

The first discussion of relative nonlinearity as a coexistence mechanism in the literature (Armstrong and McGehee 1980), did not involve life-history differences, but instead obtained relatively nonlinear growth rates from different nonlinear functional responses of two consumer species to a common resource. Endogenous consumer-resource cycles drove fluctuations in competition. It is also claimed in Armstrong and McGehee (1980) that it is possible for relative nonlinearity to support an unlimited number of species on a single fluctuating resource. Although we do not doubt this claim, we note that quadratic nonlinearities alone do not allow stable coexistence of more than two species in the absence of other stable coexistence mechanisms (Chesson 1994), and it is not clear whether biologically realistic scenarios exist that allow strong stable coexistence of more than two species on a single fluctuating resource by relative nonlinearity alone. Such coexistence would have to be based on large higher order nonlinearity differences between species. In the studies reported here, the storage effect is always present along with relative nonlinearity, and is critical to multispecies coexistence. For the two-species case Abrams and Holt (2002), showed that relative nonlinearity created by functional response differences and endogenous cycles can have

comparable strength to resource partitioning, but they note also the difficulty of obtaining

coexistence of more than two species from relative nonlinearity alone.

Although the study of coexistence based on variation from endogenous population

fluctuations alone is an interesting intellectual exercise, there is reason to question its

relevance to nature. In nature, environmental fluctuations are always present, and can be

expected to interact with endogenous forces leading to the kinds of fluctuations in

competition that drive the relative nonlinearity coexistence mechanism (Kimball et al.

2012). A more serious exercise for understanding coexistence in nature would focus not

on what endogenous cycles can do alone but how endogenous forces might interact with

temporal environmental variation to generate the fluctuations in competition actually

observable in nature. In models with linear per-capita growth rates, which include Lotka-

Volterra models and their discrete-time counterparts, Ripa & Ives (2003), and

Ruokolainen & Ripa (2012) have studied how environmental variation contributes to

population fluctuations. Extensions to models with nonlinear per capita growth rates

would be valuable for better understanding of coexistence from relative nonlinearity.

Our studies have depended on the ability to understand the separate effects of the

mechanisms in the presence of each other. This would be impossible without a suitable

method of quantifying coexistence, such as we use here. Moreover, the method that we

use has the ability to increase understanding the mechanisms. For instance, the precise

representation of the community average relative nonlinearity leaves no doubt as to the

requirements for the mechanism to promote coexistence. Verbal descriptions of the

functioning of a mechanisms try to define its requirements based on the assumptions that

seem necessary for it to work, but this approach cannot demonstrate the actual necessity and sufficiency of purported requirements.

Our findings have much relevance to empirical studies of the role of recruitment variation in species coexistence. Empirical work on this topic has focused on the storage effect alone (Cáceres 1997, Kelly and Bowler 2002, Descamps-Julien and Gonzalez 2005, Facelli et al. 2005, Adler et al. 2006, Angert et al. 2009, Chesson et al. 2011). However, our work shows the potential for major contributions to coexistence, which can be positive or negative, from relative nonlinearity with the potential to alter the conclusions from such studies. Of most importance would be situations in which the species being investigated differ greatly in life-history traits, such as life span, that can cause major nonlinearity differences between species in their per capita growth rates. Further considerations, as highlighted by our results, are correlations between species in their responses to environmental fluctuations and differences between species in sensitivities to those fluctuations.

We have focused our investigation on iteroparous species such as perennial plants, but the same phenomena can be expected in species with seasonal recruitment, as long as these species have a persistent stage in the life history (Kuang and Chesson 2008). The presence of the persistent stage provides the buffered population growth that can lead to the storage effect (Chesson 1994), and differences between species in the longevity of the persistent stage can lead to relatively nonlinear growth rates, and potentially the relative nonlinearity coexistence mechanism, as demonstrated here. An extraordinary diversity of organisms have persistent life stages. In annual plants, the persistent stage is the seed in the common case where between-year dormancy is present

with a seed bank (Adondakis and Venable 2004, Facelli et al. 2005) Relative

nonlinearity based on both fluctuations in competition and apparent competition have

been demonstrated for such annual plants systems (Kuang and Chesson 2008), as has the

storage effect (Chesson and Kuang 2010).

Arthropods may have between-year diapause, for example insects, especially

from high latitude regions. Zooplankton can have dormant progagule pools and their

long-lived egg banks establish overlapping generations (Cáceres 1997). Even single-cell

organisms such as phytoplankton can form resting cysts, which buffer population growth

through unfavorable environments (Nehring 1995). Thus, there is every reason to expect

that the phenomena discussed here are general for a wide range of communities.

Although the specific findings of this work are likely to depend somewhat on the specific

details of the system at hand, the generic nature of the summary dynamical Eq. (5) is

likely to preserve key elements of our analysis provided that competition depends directly

on the environmental responses of the species, as well as their densities, as it does here.

Appendix I

Chesson (1989), Chesson (1994) and Chesson (2003) provide the basic analysis of the lottery model, which is elaborated here to provide formulae needed for our analyses. While Chesson (1989) provides a complete analysis of the lottery model for the two species case, Chesson (1994) provides the general theory for multispecies competition in a variable environment for models of the form

$$r_j(t) = g_j(E_j(t), C_j(t)) \tag{A.1}$$

where g_j is an arbitrary continuously differentiable function. The lottery model and other models that take the form given here by Eq. (5) are special cases of this general model. Chesson (2003) focuses on models given by Eq. (5), which are general models for recruitment variation, with the lottery model as a special case. Many of the formulae that we need are available directly from Chesson (1989, 1994 and 2003). However, the emphasis in Chesson (1994 and 2003) is on the case where the environmental response variances are the same for all species. That assumption is inadequate for our purposes here. In these appendices we explain the pertinent results in these previous works, and extend and adapt them for our needs.

These previous works all rely on quadratic approximation of Eq. (A.1). The resulting expressions for the invasion rates, $\bar{r}_i$, and their division in contributions from different mechanisms are accurate to $o(\sigma^2)$ where σ^2 can be interpreted here as the maximum value of the σ_j^2 across species. For the lottery model, the only assumption needed for this to apply is that the μ_j differ between species by no more than $O(\sigma^2)$. The formulae for species coexistence in the lottery model show that this assumption is valid in the interior and boundary of the coexistence region. Simulations, and Hatfield and

Chesson (1989), show that high numerical accuracy is achieved the parameter range considered here with σ^2 no more than 1.

Chesson (2003), Table 1, gives the formulae components of the invasion rate $\bar{r}_i$, $\eta_i - \bar{\eta}_s^{\{s \neq i\}}$, ΔN_i and ΔI_i for general models obeying Eq. (5), which includes the lottery model. However, term ($\eta_i - \bar{\eta}_s^{\{s \neq i\}}$) is denoted $\bar{r}_i'$ in Chesson (2003), and is given by the formula

$$\begin{aligned} \eta_i - \bar{\eta}_s^{\{s \neq i\}} &= \mu_i - \overline{\mu}_s^{\{s \neq i\}} + \tfrac{1}{2}(1 - \delta_i)\sigma_i^2 - \overline{\tfrac{1}{2}(1 - \delta_s)\sigma_s^2}^{\{s \neq i\}} \\ &= \delta\mu_i + \delta V_i \end{aligned} \qquad (A.2)$$

Appendix II now develops the particular forms of ΔN_i and ΔI_i that we need here for the two species lottery model, and appendix III does the same for the multispecies case.

Appendix II

In the two species lottery model, the formulae for the mechanisms from the quadratic approximation do not require simulation for evaluation. The relevant formulae have been derived in Chesson (1989). These formulae show that the species-level relative nonlinearity is

$$\Delta N_i = -\left[\tfrac{1}{2}(1 - \delta_i) - \tfrac{1}{2}(1 - \delta_r)\right]V(C^{\{-i\}}) = \tfrac{1}{2}(\delta_i - \delta_r)\sigma_r^2 \qquad (A.3)$$

(Eq. 39, Chesson 1989), where i the given species and r is the other species. Averaging over species, this formula gives the community average

$$\overline{\Delta N} = \tfrac{1}{4}(\delta_1 - \delta_2)(\sigma_2^2 - \sigma_1^2). \qquad (A.4)$$

Subtracting (A.4) from (A.3) gives the fitness modifying component of relative nonlinearity as

$$\delta N_i = \Delta N_i - \overline{\Delta N} = \tfrac{1}{4}(\delta_i - \delta_r)(\sigma_1^2 + \sigma_2^2). \tag{A.5}$$

The species level storage effect is given as

$$\Delta I_i = \overline{(1-\delta_s)\chi_s^{\{-i\}}}^{\{s\neq i\}} - (1-\delta_i)\chi_i^{\{-i\}} = (1-\delta_r)\sigma_{ir} - (1-\delta_i)\sigma_{ir}^2 \tag{A.6}$$

(Eq. 40, Chesson 1989). Averaging over species gives the community average storage effect as:

$$\overline{\Delta I} = \tfrac{1}{2}[(\sigma_1^2 - \sigma_{12})(1-\delta_1) + (\sigma_2^2 - \sigma_{21})(1-\delta_2)]. \tag{A.7}$$

The fitness modifying component of the storage effect is thus

$$\delta I_i = \tfrac{1}{2}[(1-\delta_r)\sigma_r^2 - (1-\delta_i)\sigma_i^2] + \tfrac{1}{2}(\delta_i - \delta_r)\sigma_{12}. \tag{A.8}$$

The stabilizing effect in two species case can be written as the following expression and is always positive:

$$\overline{\Psi} = \overline{\Delta I} - \overline{\Delta N} = \tfrac{1}{2}(1-\overline{\delta})(\sigma_1^2 + \sigma_2^2 - 2\sigma_{12}) = \tfrac{1}{2}(1-\overline{\delta})\,\mathrm{V}(E_1 - E_2) \tag{A.9}$$

Fitness inequality accounting for the coexistence mechanisms becomes

$$\xi_i = \eta_i - \overline{\eta}_s^{\{s\neq i\}} + \delta I_i - \delta N_i = \mu_i - \mu_r - \tfrac{1}{4}(d_i - d_r)\,\mathrm{V}(E_i - E_r) \tag{A.10}$$

Note that combining A.9 and A.10 we obtain a very simple formula for the recovery rate,

$$\overline{r}_i = \xi_i + \overline{\Psi} = \mu_i - \mu_r + \tfrac{1}{2}(1-\delta_i)\,\mathrm{V}(E_1 - E_2), \tag{A.11}$$

(Eq. 41, Chesson 1989), which shows that the species will always coexistence in the three species case if the μ's are the same for both species.

Appendix III

Table 1 lists the general formulae that can be used to quantify relative nonlinearity and the storage effect. As explained in the previous appendix, the two-species case is the special situation where all mechanisms can be derived analytically. For three or more species cases, quantification of the mechanisms relies at least partially on simulation. The covariance between environment and competition needed for calculating the storage effect in Eq. (16) can be obtained completely using the simulated time series values for the environmental and competitive responses. However, following the calculations in Chesson (1994) section 5.3, without applying the symmetry assumptions used there, and dividing by δ_i to obtain results on the per generation timescale, the species level storage effect becomes

$$\Delta I_i = \gamma_i \delta_i \sum_{s \neq i} \delta_s a_s \sigma_{is} - \frac{1}{n-1} \sum_{r \neq i} \sum_{s \neq i} \gamma_r \delta_r \delta_s a_s \sigma_{rs} , \qquad (A.12)$$

where $\gamma_i = 1 - \delta_i^{-1}$, and $a_s = E\left[N_s / \sum_r \delta_r N_r\right]$. Evaluation of a_s relies on simulation. This formula was found to give almost identical values to evaluation of the formula for ΔI_i in Table 1 by simulation.

Relative nonlinearity was calculated using Eq. (15), where the variance in competitive responses, $V(C^{\{-i\}})$, was found from simulation. The formula for community average relative nonlinearity is given in Chesson (2003) as

$$\overline{\Delta N} = \frac{n}{2(n-1)} \mathrm{Cov}\left(\delta_i, V(C^{\{-i\}})\right) \qquad (A.15)$$

This formula can be rearranged as follows to give Eq. (15) used here:

$$\overline{\Delta N} = \frac{1}{2(n-1)} \sum_{i=1}^{n} (\delta_i - \overline{\delta}) \, V(C^{\{-i\}})$$

But, $\delta_i - \overline{\delta} = -(n-1)(\overline{\delta}_s^{\{s \neq i\}} - \overline{\delta})$. Thus,

$$\overline{\Delta N} = \frac{1}{2(n-1)} \sum_{i=1}^{n} -(n-1)(\overline{\delta}_s^{\{s \neq i\}} - \overline{\delta}) \, V(C^{\{-i\}})$$

$$= -\frac{n}{2} \mathrm{cov}_i \left(\overline{\delta}_s^{\{s \neq i\}}, V(C^{\{-i\}}) \right)$$

(A.16)

Eq. (15), identical with A.16, has the advantage that it directly associates the resident death rates with the variance in competition that the residents create.

Appendix IV

Except in Table 3, all results in the text are given for the case of equal μ values (ln mean life time fecundity). With equal μ values, both species in any two species community coexist stably according to the lottery model provided there is any variance in the difference between their environmental responses, as can be seen from Eq. (A.11). This means that the two species studies above with equal μ values are studies where the species do stably coexist. This also means that all two-species resident communities exist for the three species studies with equal μ's (i.e. the two resident species coexist). However, stable coexistence does not necessarily occur for the three species assemblage, as one or more may not be able to invade the two-species resident community, despite being equal in μ value. This outcome is understandable given that the contributions of the coexistence mechanisms can be highly asymmetric in the cases studied in this investigation.

Our calculations presented in Table 3 show that the community average measures are not greatly sensitive to fitness inequality, justifying the focus on the equal μ case for our calculations. The combined community average mechanisms $\overline{\Psi}$ gives the average invader recovery rate, and indicates coexistence strength in terms of the fitness differences compatible with coexistence. Our question here is whether patterns observed

for how $\bar{\Psi}$ changes with the circumstances can be related to patterns of community stability defined in terms of joint population fluctuations. To consider this question, we develop here a measure of fluctuational stability

$$n\left(E\left[\prod_{j=1}^{n} N_j \right] \right)^{\frac{1}{n}}.$$ (A.17)

Taking the nth root of the expectation in (A.17) and then multiplying it by n will scale the stability measure between 0 and 1. Fluctuational stability measures the degree of fluctuation in the community in terms of how much the densities keep away from 0. If there are no fluctuations over time, and species stay at the equal constant density of $1/n$, the fluctuational stability will reach the maximum value 1. If instead, the community has large fluctuations, with some species often near zero, the measure will approach the minimum value of 0.

The two species stationary distribution, as derived by diffusion approximation (Hatfield and Chesson 1989), depends on $(\mu_1 - \mu_2)/V(E_1 - E_2)$ and δ_1 and δ_2 only. As $\bar{\Psi}$ is proportional to $V(E_1 - E_2)$, but does not involve $\mu_1 - \mu_2$ in this case, fluctuational stability should depend on $\bar{\Psi}$ when average fitnesses are different, but not necessarily otherwise. Thus, fluctuational stability should provide new insight into the effects of the coexistence mechanisms. Because the mechanisms can have strong effects on average fitness differences as well as on community average stabilizing mechanisms, summarized by $\bar{\Psi}$, patterns of fluctuational stability for μ differences fixed at 0 should give very different results, especially when such average fitness differences arising from the mechanisms would predict extinctions in the three species case with μ differences fixed at zero.

Our results shows that maximum fluctuational stability is not sensitive to the spacing of adult death rates (Supp. Fig. 4a, 5), sensitivity differences (Supp. Fig. 4, 5, 6), or correlations in the environmental responses between species (Supp. Fig. 4b, 6), in the range of situations that we have studied. Surprisingly, these results imply that, provided the conditions for coexistence are actually satisfied, maximum fluctuational stability is dependent primarily on the number of species. However, we have not studied the effects of mean sensitivity across species or mean adult death rates across species. These quantities are fixed in our analysis. Nevertheless, it is clear that maximum fluctuational stability is indeed giving different information than $\overline{\Psi}$, which measures the species average invasion rate.

Consistent with our predictions, fluctuational stability measured at equal μ values shows a very different pattern from its maximum value (Supp. Fig. 4, 5, 6). At equal μ values, fluctuational stability declines rapidly with death rate spacing (Supp. Fig. 4a, 5). This is likely to be the result of increasing average fitness differences between species introduced by relative nonlinearity. In contrast $\overline{\Psi}$ can increase with death rate spacing (Fig. 1 a&c), or at least stay at high values (Fig. 1b) at fixed μ values, not greatly different from maximum fluctuational stability. Correlation between environmental responses has a negligible effect on fluctuational stability with equal μ's. Indeed, this is predicted by the stationary distribution in the two species case because then $(\mu_1 - \mu_2)/V(E_1 - E_2) = 0$, nullifying any effect of correlation on the form of this distribution. Naturally, in this case also, sensitivity differences are unimportant, as seen in Supp. Fig. 4. However, in the three species case, sensitivity differences affect the fluctuation stability measured at equal μ values. Among all three cases, the strongest fluctuational

stability as equal μ values occurs when the shorter-lived species is more sensitive to the environment. This is also the case when relative nonlinearity can potentially equalize fitness differences between species due to the effects of δV_i, i.e. fitness inequality introduced by variance differences despite equal μ values (Supp. Fig 5, 6).
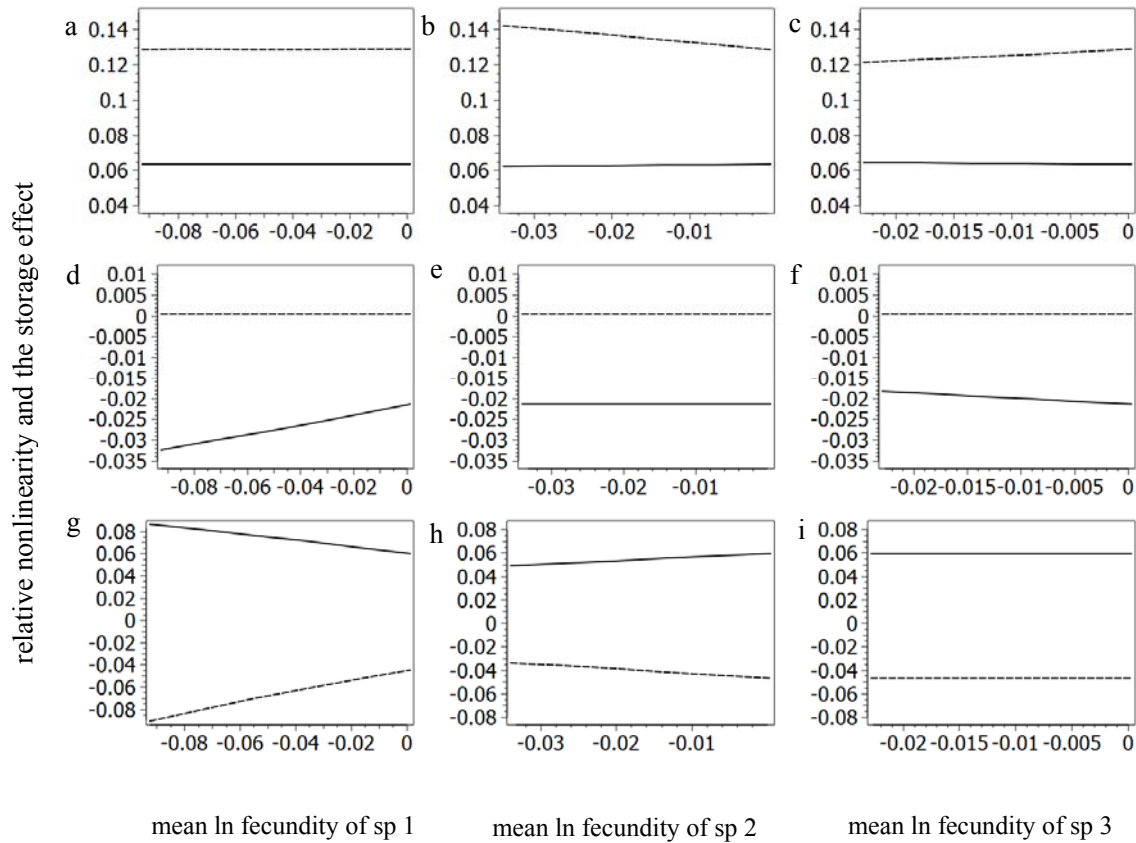
Supplementary figures
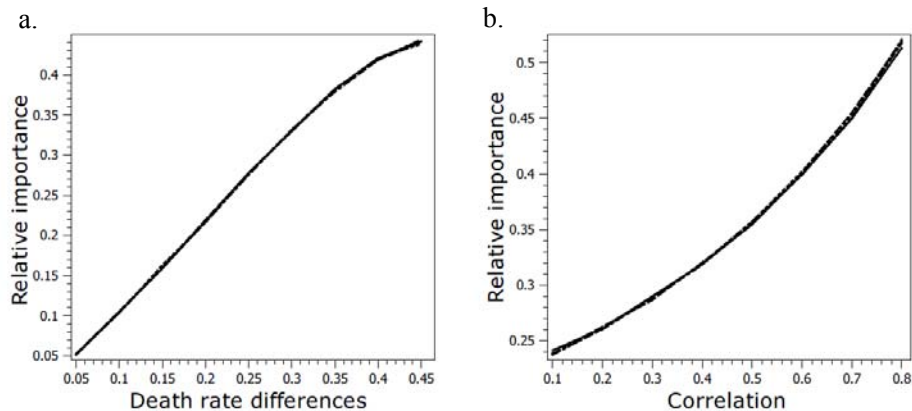
Supplement Figure 1. The relative contribution of relative nonlinearity ($-\overline{\Delta N}/(-\overline{\Delta N}+\overline{\Delta I})$) for different average variances in environmental responses (lines for $\overline{\sigma^2}$ can be seen to be essentially coincident). a) $-\overline{\Delta N}/(-\overline{\Delta N}+\overline{\Delta I})$ plotted against differences in death rate. b) $-\overline{\Delta N}/(-\overline{\Delta N}+\overline{\Delta I})$ plotted against correlation in environmental responses (ρ). *Parameters*: $\sigma_1^2:\sigma_2^2:\sigma_3^2 = 1{:}6{:}11$. For (a) $\rho = 1/3$; $\overline{\delta} = 0.5$, with $\delta_1 < \delta_2 < \delta_3$ following an arithmetic sequence and for (b) $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$. The average variances ($\overline{\sigma^2}$) for these lines are 0.1(solid line), 0.2(dashed line), 0.3(dotted line), 0.4(dashed dot line), 0.5(dashed dot dot line).
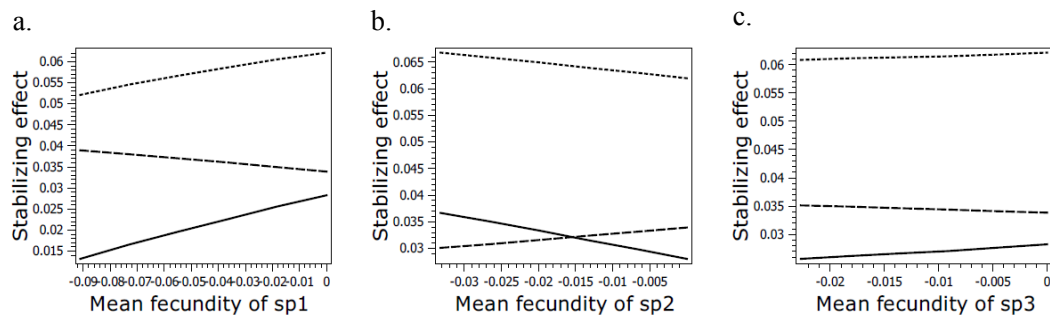

Supplementary Figure 2. The stabilizing effect of relative nonlinearity (solid line), storage effect (dash line) and the overall stabilizing mechanism (dot line) as mean ln fecundity (μ) differences between species change. In each graph above, μ values for each species are in turn varied from its invasion boundary to the coexistence central ($\mu = 0$ for all species),while μ values for the rest are kept 0. In (a), the stabilizing effects are plotted against the mean fecundity of species 1:the least sensitive and longest-lived species; In (b), the stabilizing effects are plotted against the mean fecundity of species 2: the species with median sensitivity and median longevity; In (c), the stabilizing effects are plotted against the mean fecundity of species 3: the

most sensitive and shortest-lived species(c). *Parameters*: $\rho = 0.6$; $\overline{\sigma^2} = 0.5$; $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$; $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$.


Supplement Figure 3. Species level coexistence mechanisms as mean ln fecundity (μ) differences change: solid lines are for the storage effect and dashed lines for relative nonlinearity. Rows 1-3 of the table are the mechanism measures respectively for species 1-3. Columns 1-3 correspond to the species whose mean ln fecundity is varied, as indicated in x-axis label.

Parameters: $\rho = 0.6$, $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$, $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$. (Each line is drawn by connecting 6 equally spaced points.)

a.

b.
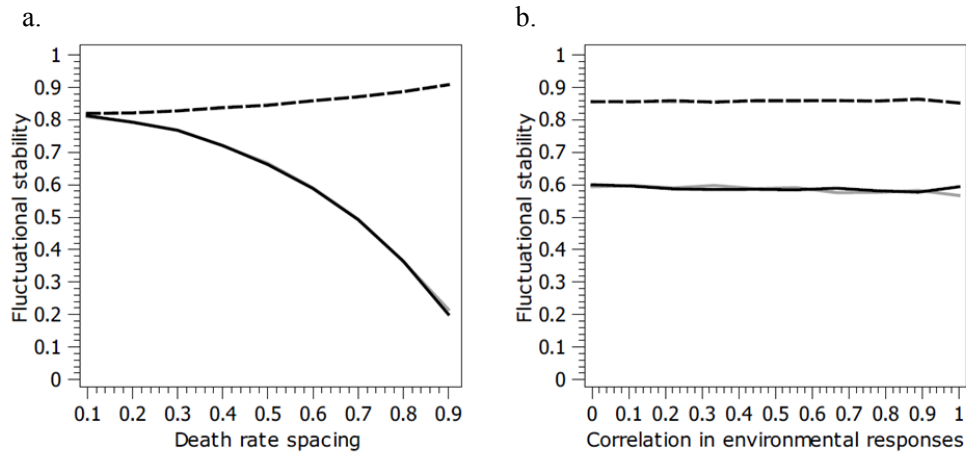
Supplementary Figure 4. Comparisons between the fluctuational stability with equal μ values (solid line) and the maximum fluctuational stability with different μ values (dashed line) in the two species case. In (a) fluctuational stability is plotted against death rate spacing. In (b) the fluctuational stability is plotted against ρ (pairwise correlation in environmental responses). The result is insensitive to which species is more sensitive to the environment. *Parameters*: $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 = 1 : 2$ (black lines) or 2:1 (grey lines), for (a) $\rho = 0.3$, $\overline{\delta} = 0.5$, and for (b) $\delta_1 = 0.2$, $\delta_2 = 0.8$.

a.

b.

c.
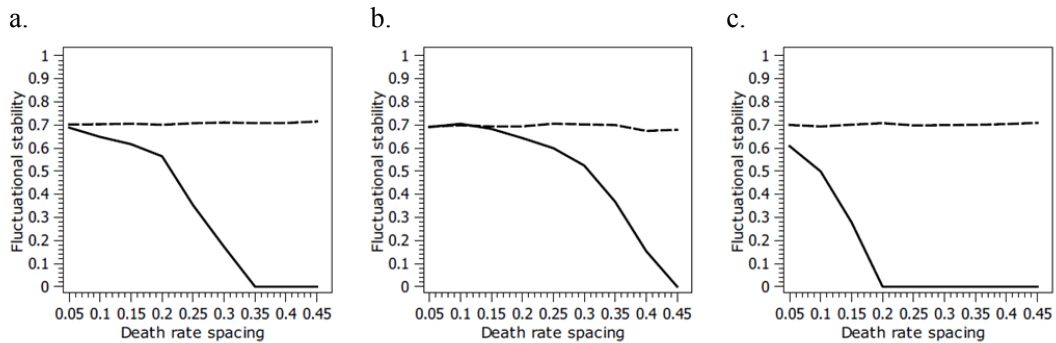
Supplementary Figure 5. Trends of the fluctuational stability as death rate spacing increases in the three species cases. In each figure, comparisons are made between fluctuational stability with equal μ values (solid line) and the maximum fluctuational stability with different μ values (dashed line). Between figures, comparison are made between (a) the case that species have equal sensitivities to the environmental fluctuation, (b)the case that shorter-lived species are more sensitive, and (c) the case that longer-lived species are more sensitive. *Parameters*: $\rho = 1/3$, $\overline{\delta} = 0.5$, $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1:6:11$ for (b) or 11:6:1 for (c).

a.

b.

c.
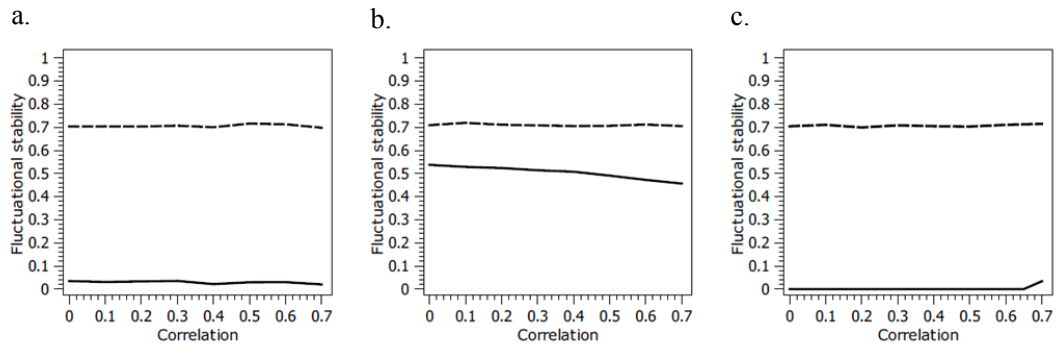
Supplementary Figure 6. Trends in fluctuational stability as correlation between species in environmental responses (ρ) increases. In each figure, comparisons are made between fluctuational stability with equal μ values (solid lines) and the maximum fluctuational stability with different μ values (dashed lines). (a) species have equal sensitivity to environmental variation, (b)shorter-lived species are more sensitive, and (c) longer-lived species more sensitive. *Parameters*: $\delta_1 = 0.2$, $\delta_2 = 0.5$, $\delta_3 = 0.8$. $\overline{\sigma^2} = 0.5$, $\sigma_1^2 : \sigma_2^2 : \sigma_3^2 = 1{:}6{:}11$ for (b) or $11{:}6{:}1$ for (c).

References:

Abrams, P. 1984. Variability in resource consumption rates and the coexistence of competing species. Theoretical Population Biology **25**:106-124.

Abrams, P. A. and R. D. Holt. 2002. The impact of consumer-resource cycles on the coexistece of competing consumers. Theoretical population biology **62**:281-295.

Adler, F. R. 1990. Coexistence of two types on a single resource in discrete time. Journal of mathematical biological **28**:695-713.

Adler, P. B., J. HilleRisLambers, P. C. Kyriakidis, Q. F. Guan, and J. M. Levine. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proceedings of the National Academy of Sciences of the United States of America **103**:12793-12798.

Adondakis, S. and D. L. Venable. 2004. Dormancy and germination in a guild of Sonoran Desert annuals. Ecology **85**:2582-2590.

Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. Proceedings of the National Academy of Sciences **106**:11641-11645.

Armstrong, R. A. and R. McGehee. 1980. Competitive Exclusion. The American Naturalist **115**:151-170.

Bulmer, M. G. 1985. Selection for iteroparity in a variable environment. The American Naturalist **126**:63-71.

Cáceres, C. E. 1997. Temporal variation, dormancy, and coexistence: A field test of the storage effect. Proceedings of the National Academy of Sciences of the United States of America **94**:9171-9175.

Charnov, E. L. 1991. EVOLUTION OF LIFE-HISTORY VARIATION AMONG FEMALE MAMMALS. Proceedings of the National Academy of Sciences of the United States of America **88**:1134-1137.

Charnov, E. L. 1993. Life history invariants: Some exploration of Symmetry in Evolutionary Ecology. Oxford University Press, USA.

Charnov, E. L. 1997. Trade-off-invariant rules for evolutionarily stable life histories. Nature **387**:393-394.

Chesson, P. 1982. The stabilizing effect of a random environment. Journal of Mathematical Biology **15**:1-36.

Chesson, P. 1994. Multispecies competition in variable environments. Theoretical population biology **45**:227-276.

Chesson, P., N. J. Huntly, S. H. Roxburgh, M. Pantastico-Caldas, and J. M. Facelli. 2011. The storage effect: definition and tests in two plant communities.*in* C. K. Kelly, M. G. Bowler, and G. A. Fox, editors. Temporal dynamics and ecological process. Cambrige University Press, In press.

Chesson, P. and J. J. Kuang. 2010. The storage effect due to frequency-dependent predation in multispecies plant communities. Theoretical Population Biology **78**:148-164.

Chesson, P. and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems The American Naturalist **117**:923-943.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**:343-366.

Chesson, P. L. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical population biology **64**:345-357.

Chesson, P. L. 2008. Quantifying and testing species coexistence mechanisms. Unity in Diversity: Reflections on Ecology after the legacy of ramon margelef.

Comins, H. N. and I. R. Noble. 1985. Dispersal, Variability, and Transient Niches: Species Coexistence in a Uniformly Variable Environment. The American Naturalist **126**:706-723.

Descamps-Julien, B. and A. Gonzalez. 2005. Stable Coexistence in a Fluctuating Environment: An Experimental Demonstration. Ecology **86**:2815-2824.

Ellner, S. 1984. Asymptotic behavior of some stochastic difference equation population models. Journal of Mathematical Biology **19**:169-200.

Facelli, J. M., P. Chesson, and N. Barnes. 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology **86**:2998-3006.

Hatfield, J. S. and P. L. Chesson. 1989. Diffusion analysis and stationary distribution of the two-species lottery competition model. Theoretical population biology **36**:251-266.

Hatfield, J. S. and P. L. Chesson. 1997. Multispecies lottery competition: a diffusion analysis. Pages 615-622 *in* C. H. Tuljapurkar S. , editor. Structured Population Models in Marine, Freshwater, and Terrestrial Systems. . Chapman and Hall, New York.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Huisman, J. and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. Nature **402**:407-410.

Huisman, J. and F. J. Weissing. 2002. Oscillations and chaos generated by competition for interactively essential resources. Ecological Research **17**:175-181.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist **95**:137-145.

Kang, Y. and P. Chesson. 2010. Relative nonlinearity and permanence. Theoretical Population Biology **78**:26-35.

Kelly, C. K. and M. G. Bowler. 2002. Coexistence and relative abundance in forest trees. Nature **417**:437-440.

Kimball, S., J. R. Gremer, A. L. Angert, T. E. Huxman, and D. L. Venable. 2012. Fitness and physiology in a variable environment. Oecologia **169**:319-329.

Kuang, J. J. and P. Chesson. 2008. Predation-competition interactions for seasonally recruiting species. The American Naturalist **171**:119-133.

Kuang, J. J. and P. Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. Ecology **90**:170-182.

Loreau, M. 1992. Time scale of resource dynamics and coexistence through time partitioning. Theoretical Population Biology **41**:401-412.

May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. American Naturalist **107**:621-650.

May, R. M. 1974. On theory of niche overlap. Theoretical Population Biology **5**:297-332.

Munday, P. L. 2004. Competitive coexistence of coral-dwelling fishes: The lottery hypothesis revisited. Ecology **85**:623-628.

Needham, T. 1993. A Visual Explanation of Jensen's Inequality. The American Mathematical Monthly **100**:768-771.

Nehring, S. 1995. Dinoflagellate resting cysts as factors in phytoplankton ecology of the North Sea. Helgoländer Meeresuntersuchungen **49**:375-392.

Pacala, S. W. and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist **143**:222-257.

Real, L. A. and S. Ellner. 1992. Life history evolution in stochastic environments: a graphical mean variance approach. Ecology **73**:1227-1236.

Ripa, J. and A. R. Ives. 2003. Food web dynamics in correlated and autocorrelated environments. Theoretical Population Biology **64**:369-384.

Ruokolainen, L. and J. Ripa. 2012. The strength of species interactions modifies population responses to environmental variation in competitive communities. Journal of Theoretical Biology **310**:199-205.

Schreiber, S. J., M. Benaim, and K. A. S. Atchade. 2011. Persistence in fluctuating environments. Journal of Mathematical Biology **62**:655-683.

Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio **58**:29-55.

Turelli, M. 1981. Niche overlap and invasion of competitors in random environments I: models

without demographic stochasticity Theoretical Population Biology **20**:1-56.

Appendix B

A structured lottery model for species coexistence in a variable environment: general coexistence mechanisms for species with complex life histories.

Chi Yuan[1] and Peter Chesson[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, United States

Corresponding author

C. Yuan: cyuan@email.arizona.edu, Ph: (520) 621-1889

P. Chesson: pchesson@u.arizona.edu, Ph: (520) 621-1451

Abstract

Models of species coexistence tend to be of two opposite sorts. Abstract models do not have the life-history detail to allow the investigation of much interesting biology. Analyses of complicated models often have difficulty revealing the details of coexistence mechanisms. Here we show that techniques of quantifying coexistence mechanisms developed for simpler models can also apply to more complex models, allowing study of how life-history details affect species coexistence. In a new cohort-based size-structured lottery model, uniquely, we have both reproduction and growth as functions of varying environmental factors and competition. Variation in both processes lead to stable coexistence through distinct storage effects when functioning alone. Acting together and positively correlated in the model, they are strongly synergistic. Our results show that for coexistence, the most important aspect of a species' life history is the set of life stages sensitive to physical environmental factors and competition. The size dependency in life history processes—such as an offspring size, growth rate, fecundity rate, and mortality rate—determines the average contribution of critical history processes to population growth. If individual growth contributing more on average to population growth than reproduction, storage effect in growth will be more important than storage effect in reproduction, and vice versa. Beside storage effects, variable environment leads to shifts in size structure as species' densities change. Variation in reproduction and variation in growth drive size structure in opposite directions. Either can promote or undermine species coexistence, depending on whether the change in size structure on decline to low density favors population growth, and hence recovery from low density. Quantification of coexistence mechanisms reduces the understanding of complexity of life-history

strategies into population level measurement, which turns out to be no much complicated than in simple models.

Introduction

It has long been recognized that stable species coexistence stems from different species using the environment differently (Chesson 2000). Many hypotheses of coexistence mechanisms are proposed (Palmer 1994, Chesson 2000, Wright 2002). Among them, coexistence as a result of environmental variation has often been seen as key. It is important to recognize that all species live in constantly changing environments. Empirical studies document species- specific temporal variation in critical life history processes in a variety of systems including tropical forests, dessert annuals, coral reefs, fresh water zooplankton (Venable et al. 1993, Cáceres 1997, Soong et al. 2003, Wright et al. 2005, Chesson et al. 2013), suggesting that species partition temporal variation in the environment. Meanwhile, an extraordinary diversity of organisms have persistent life stages that allow persistence through unfavorable conditions (buffered population growth), e.g. prolonged life span of long-lived organisms and dormant stages of short-lived organisms (Danks 1987, Nehring 1995, Pake and Venable 1996, Cáceres 1997, Venable 2007), which can be the bet-hedging strategies of life-history theory (refs).

Sophisticated theories of species coexistence in variable environments exist. Yet there are challenges in applying theory to study empirical system majorly due to the contrast between simplicity in model assumptions and complexity in natural world. The key models used to develop the theories have been relatively simple, which makes them more tractable and understandable. The lottery model, for example, provides fundamental understanding of how temporal environmental variation can promote species coexistence (Chesson and Warner 1981). The model reduces the life-history of perennial iteroparous

organisms, such as forest trees, to their bare essence: adults produce propagules which compete to establish as adults. Propagule competition is completely a lottery, meaning that the success of species is proportional to the number of its propagules. The assumption for its base is simple: namely all individuals of a species are identical, and reproduction, propagule competition and establishment as an adult can be compressed into one unit of time. The simple model leaves out many detailed biology.

Questions arise on whether all the complexities in life history matter for coexistence. If not, more complicate model is unnecessary. We will illustrate our ideas using forest trees, but our conclusion is general. Coexistence of plants in nature are often puzzling because they rely on a relatively small number of resources, yet have high diversity (Silvertown 2004). Forests trees, in particular, have complex life histories that pose challenges in both modeling and experiment (Clark and Clark 1992). Yet these complicated life histories carry much information about differences between species in ecological strategies (Condit et al. 2006). Meantime, long-term forest studies show evidence of enormous temporal variation in several life-history parameters, including reproduction, seed germination, and tree growth (Clark and Clark 1994, Wright et al. 2005). These findings raise the question of how temporal variation in these different life history processes affects species coexistence.

There have been various attempts to relate the ordinary lottery model to actual forest systems, e.g. coexistence of species with differing tendencies to recruit following fires in Australian eucalypt forests (Comins and Noble 1985); dynamics of tropical with temporal patterns of masting (Hubbell (2001)). More recently, Usinowicz et. al. (2012) extended the lottery model to a two-stage model and use it to study coexistence of tropical trees in Barro Colorado Island (BCI), Panama. These previous studies, along with much other

empirical work, indicate strong potential for environmental variation to contribute to diversity maintenance in forests (Wright et al. 2005). However, in all cases, tree life histories are represented in seriously contracted forms. The match between the model and the fundamental idea under test remains tenuous.

In this study, we enhance the ordinary lottery model, allowing it to capture the complex life histories of communities studied and yet summarize the complexity with a few critical parameters. First of all, our new model is size explicit. Size, either for juveniles, or established individuals, has had a prominent role in the formulation of life history strategies (Clark and Clark 1992, Thomas 1996, Westoby et al. 2002, King et al. 2006, Muller-Landau et al. 2006, Iida et al. 2013). Size is closely related to other important properties of trees including competitive ability, growth rate, fecundity and mortality rate. Introducing size into a model allows interesting life histories to be represented. It can capture more biological details in the seedling recruitment process than an unstructured model, and can represent post-recruitment growth processes. The latter is the fundamental as we are particularly interested using the new model to study the effects of tree growth dynamics on species coexistence. While temporal variation in tree growth has been quite often observed (Clark and Clark 1994, Enquist and Leffler 2001, Nath et al. 2006, Soliz-Gamboa et al. 2012), its role in species coexistence is not understood theoretically. Yet it seems reasonable to expect that temporal differentiation between species in individual growth should promote coexistence in a similar way to temporal differentiation in recruitment.

Using the new size-structured model, we are able to identify aspects of life history strategies that affect species coexistence the most: the sets of life stages sensitive to both physical environmental factors and competition. Variation in reproduction and individual

growth can both promote coexistence through distinct storage effects. The key effects of a complex life-history on coexistence through the storage effect is through simply determining whether processes most sensitive to environment can contribute more on average to population growth. Beside the storage effects, the mean size structure of a species shift as its densities change, which can be either promoting or undermining coexistence. Interestingly, variation in growth and variation in reproduction will drive species' mean size structure in opposite directions when species drops to low density. Shift in size structure will promote coexistence if size structure for the population at low density allows species to take more advantages of the demographic schedules. Otherwise, it will undermine coexistence.

The model

The model describes a forest community of many species, and each species consists of individuals of different sizes. The basic workings of the model are defined in Figure 1, the parameters for the model are in table 1, and the detailed formulae behind the model are in table 2. Here we give the narrative description of the model. We assume that area of the whole forest is conserved, and the size of each individual tree is given by an area, reflecting a share of the total resources of the forest available to it. Summing the area of all individuals of all sizes leads to the constant area of the whole forest. Space is used as a general measure of the overall resources and all individuals compete for space.

The model works in discrete time. In each unit of time trees die according to species specific size-dependent mortality functions. Death frees space, which the living compete for. Competition comes from two sources: (1) newly germinated seedlings that need space to establish; (2) established individuals, which need space to grow. Competition between individuals for this newly available space occurs according to a lottery formula.

Thus, the allocation of space to an individual is proportional to its demand for space divided by the total demand from all individuals of all species in the forest. A fecundity function determines the number of seedlings competing to establish. It is a species-specific function that depends on both the size of an individual and the physical environmental. A competitiveness function determines the demand for space of each individual, which is the new area an individual would acquire without resource limitation. The competitiveness function is also species-specific depending on both size and the physical environment, like the fecundity function. No variation between individuals of the same age and species occurs. The model is cohort-based. The fate of any individual is predictable based on its species, cohort, and the shared environment of all individuals. Details are described in below.

Critical variables in the model are the total available space, $S(t)$, from deaths during the interval t to $t + 1$, and the total demand, or requirement, for space, $R(t)$ (details in T. 2 Eq. 2-7). As explained above, this demand for space is the total new space needed to achieve the largest potential of reproduction and growth under unlimited space supply. Since the space available is not unlimited, competition occurs. The magnitude of competition $C(t)$ is evaluated as the ratio of demand to supply on the log scale (T. 2 Eq. 8), also referred as the competitive response. Individuals of all species and sizes compete in same resource pool, and competition reduces their actual establishment and growth.

The key dynamical components of the model are recruitment to the seedling cohort, and subsequent growth of individuals in the established cohorts. A tree in cohort c of species j has size a_{jc}, which does change with time but t is omitted for notational simplicity. Before competition, seedling produced by N_{jc} individuals in cohort c of

species j depends on two components (T.2 Eq. 3). The first term, fecundity schedule $k_{a_{jc}}$,

determines the size-dependency in fecundity, which is time invariant and further

weighted by the competitiveness in seedling establishment c_{sj}. The other factor $e^{E_{bj}(t)}$

captures fluctuation in reproduction due to environmental variation, where the quantity

E_{bj} is defined as the environmental response in reproduction. Newly established seedling

has initial size a_{sj}.

Table 1. General notation

Symbol	Definition
C	Competitive responses
R	Total demand for resource from seedling recruitment and tree growth
S	Total available space, from death of trees
c	Index for cohort
j	Index for species, in particular i for invader, r for resident
p	Total number of species in the community
a_{jc}	Size of individuals in cohort c of species j
a_{nj}	Size of individual in the seedling cohort of species j
$k_{a_{jc}}$; $c_{a_{jc}}$	Size-dependent fecundity schedule and growth (competitive) schedule
E_{bj}, E_{gj}	Environmental response in reproduction and in growth respectively
$k_j(a_{jc}, t)$	Fecundity per individual in cohort c of species j
c_{sj}	Competitiveness in seedling establishment
N_{sj} ; N_{nj}	Density of seedling germinated and established respectively
N_{jc}	Density of cohort c of species j
$m_{a_{jc}}$	Size-dependent mortality schedule
A_j ; A_{bj} ; A_{gj}	Total Area, area of the new seedling cohort, and established cohorts
r_j	The population growth rate of species j evaluated as changes in $\ln A_j$
β_j	The scaling factor, sensitivity of growth rate r_j to competition.
$\bar{r}_i$	Long-term low density growth rate of invader species
ξ_i	Average fitness differences between invader and resident
$\bar{A}$	The overall stabilizing effect
ΔS	Mean effect of size structure

ΔE	Mean environmental effect
ΔI; ΔI_b; ΔI_g	The overall storage effect; storage effect in reproduction; storage effect in growth
χ_b; χ_g	Covariance between E_b and C; Covariance between E_g and C;
ψ_b; ψ_g	storage coefficient for buffer in reproduction, and buffer in growth
θ_b; θ_g	Sensitivity of C to E_b; Sensitivity of C to E_g
p_s, p_b, p_{bg}, p_g	Proportional contribution of survival, reproduction, seedling growth, sapling growth to population growth

Table 2. Model details

Process	Formula	Eq
Space occupied by species j at time t	$A_j(t) = \sum_c a_{jc}(t)N_{jc}(t)$	0
Death release spaces	$S = \sum_{c,j} N_{jc} a_{jc} m_{a_{jc}}$	0
Number of Seedling germinated	$N_{sj}(t+1) = \sum_c c_{sj} k_{a_{jc}} e^{E_{bj}(t)} N_{jc}$	0
Seedling size	$a_{nj} = a_{sj} + c_{a_{sj}} e^{E_{gj}}$	1
Demand for space from seedling	$R_s = \sum_j \left(a_{sj} + c_{a_{sj}} e^{E_{gj}} \right) \sum_c c_{sj} k_{a_{jc}} e^{E_{bj}} N_{jc}$	2
Demand for space from tree growth	$R_g = \sum_j \sum_c c_{a_{jc}} e^{E_{gj}} \left(1 - m_{a_{jc}}\right) N_{jc}$	2
Requirement for space	$R = R_s + R_s$	2
Competitive responses	$C = \ln\left(\dfrac{R}{S}\right)$	3
Density of seedling established	$N_{nj} = N_{sj} e^{-C} = \sum_c c_{sj} k_{a_{jc}} e^{E_{bj}-C} N_{jc}$	4
Growth of existing cohorts	$a_{jc}(t+1) = a_{jc}(t) + c_{a_{jc}} e^{E_{gj}-C}$	5
Space occupied by species j at time t+1	$A_j(t+1) = a_{nj} N_{nj} + \sum_c a_{jc}(t+1) s_{a_{jc}} N_{jc}(t)$	5

(1) Forest at time t

(2) Number of Seedling produced, Eq.

(3) Space opened up after tree death $Sp(t)$,

(4) Seedling establishment (Eq. 9) and growth (Eq. 4)
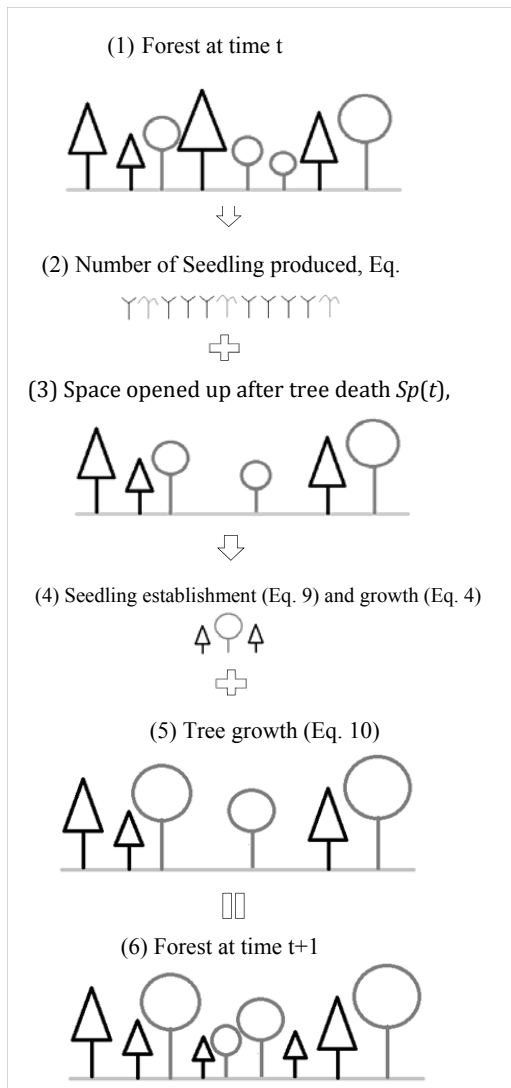
(5) Tree growth (Eq. 10)

(6) Forest at time t+1

Figure 1. The cohort-based size-strucutured lottery model. This conceptual graph describes the processes happened in one unit of time for the forest modeled in this study. (1) At time t, space are occupied by two species with individuals of different sizes. (2) The amount of seedlings produced depends on both the size of the mother plant and the physical environmental, details in Eq.0. (3) Death removes individuals and the space available is limited so that both the incoming new cohorts in (2) and the surviving individuals in (3) need to compete for it. (4) Competition reduces the actual number of seedling established (Eq.4) and the size of seedling depend on environmental factors Eq.1. (5) The growth of established trees is proportional to environment and inversely proportional to competition as in Eq.5. The size of tree and seedling symbols meaningfully represent dynamic in tree growth and seedling recruitment. In this snapshot of example, one species (black) is experiencing favorable environment for reproduction and the other species (grey) is experiencing favorable environment for growth.

Individuals in all cohorts will grow. The potential growth without competition for cohort c of species j is determined by two components: a size-dependent growth schedule $c_{a_{jc}}$, also called the competitiveness schedule; and the temporal fluctuation in growth $e^{E_{gj}(t)}$, where E_{gj} is defined as the environmental response in growth. We assume seedling growth after germination is not subject to competition as competition already occurred during their establishment (T. 2 Eq. 4). Unlike seedlings, the growth of individuals in the established cohorts is reduced by competition (T.2 Eq. 10). Only trees escaped the death, in a remaining proportion of $1 - m_{a_{jc}}$, can grow.

The population growth rate of species j is evaluated as change in log area occupied by the whole population from one time to another as:

$$r_j(t+1) = \ln A_j(t+1) - \ln A_j(t) \qquad\qquad 5$$

where A_j is the area of species j (T. 2. Eq 11).

The long-term growth rate is obtained by averaging Eq 5 overtime, with proper scaling factor between species, for species at low density.

$$\overline{r_j} = \frac{E(r_j)}{\beta_j} = \frac{1}{\beta_j} \frac{\lim_{t' \to \infty} \sum_{t=1}^{t'} r_j(t)}{t'} \qquad\qquad 5$$

As will be explained latter, the low-density growth rate is a critical measure for species coexistence. The purpose of parameter β_j is to put growth rate of species with different sensitivities to competition on the same scales of comparison, referred as the natural scale.

In this model, variation can occur during both seedling recruitment and tree growth. By modeling environmental response in reproduction E_b and the environmental response in

growth E_g separately, we allow these two processes to capture different environmental

cues. Both environmental responses and competitive response are measured on the log

scale for more accurate representation of the results in a lottery model (Chesson 1982).

Among all three life history process — reproduction, growth and mortality — mortality is

the only process that does not directly depend on environment or competition. However,

as growth does depend on the environment and competition in general, the size

dependence of mortality leads to an indirect effect of the environment and competition on

the mortality.

For simplicity, we assume two species in the community have identical demographic

schedules and mean life history traits, which means that the scaling factor β is the same

for both species. These cases resemble the guild of species with similar ecology in the

community. We choose a typical combination of tree demography schedules as a baseline

to illustrate the model: a linear fecundity schedule, an U-shaped mortality schedule, and a

hump-shaped growth schedule for both species (solid lines, Fig. 2). The linear fecundity

schedule captures the trend that larger individuals produce more seeds than smaller ones.

We can set different size thresholds for the initial reproduction to represent the different

degree of delay in reproduction (Fig. 2a), common for forest trees (Thomas 1996). A U-

shaped mortality schedule captures the trend that mortalities are higher for both the

smallest and largest trees than the intermediate-sized ones (Fig. 2b). Being small is most

vulnerable to diseases and predation, while largest trees are usually old and face

senescence (King et al. 2006). The hump-shaped growth schedule reflects an advantage

in competition for resources as plants grow larger; But after some threshold, the capacity

to grow decreases when maintenance costs, such as evapotranspiration, limit the ability to

expand further (Westoby et al. 2002). We will vary the seedling sizes as the initial point of growth.

We further compare the demographic schedules in baseline cases, as references, with size-independent ones (dashed lines, Fig 2). These comparisons specifically address the consequences of changing one particular demographic schedule from the reference schedule to a size-insensitive one (dashed lines, Fig. 2) while all other schedules remain the same as the reference. Constrained are applied so size-dependent and their corresponding size-independent demographic schedule have identical population average values. The detailed formulae and parameterization of the demographic schedules are described in Appendix I. Though these particular shapes are chosen, the models is not limited to the possible shapes of demographic schedules (Appendix I). A follow up study will take more serious consideration of the comparison between contrasting life history schedules between species (Yuan and Chesson, in progress). For now, a comparison between flat and size-sensitive demographic schedule is an important step to figure out

whether the shape has an effect at all on species coexistence.
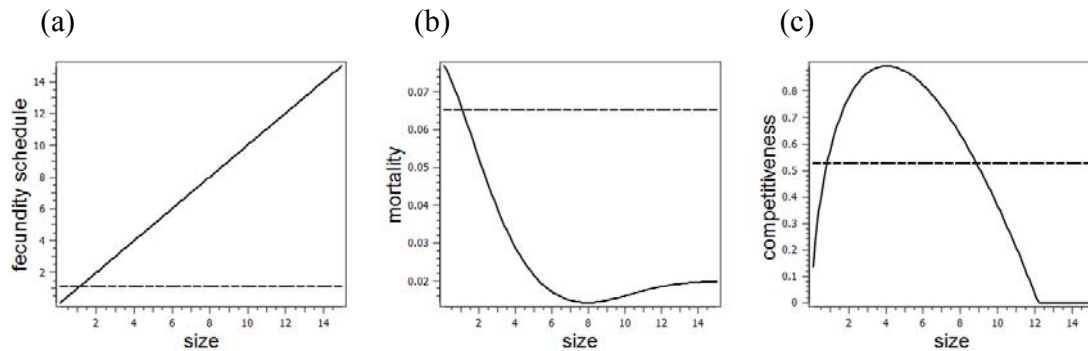
(a) (b) (c)

Figure 2. Examples of demographic schedules investigated in this study. (a) Linear increasing fecundity schedule (solid line) vs size insensitive schedule (dashed line). (b) U-shaped mortality schedule (solid line) vs size insensitive mortality schedule (dashed line). (c) Hump-shaped competitive schedule (solid line) vs size insensitive competitive schedule (dashed line). Detailed parameters setting is described in Appendix I.

Theory development

The stability of coexistence is measured by the tendency of species to recover when dropped to low density. Using the invasibility analysis (Turelli 1981, Chesson 1994), we can measure the average rate, as in Eq5, at which a species recovers from low density in the presence of its competitors fluctuating in a stationary way. The species perturbed to low density is called the invader species and the species fluctuating around equilibrium is called the resident species. Chesson (Chesson 2003, 2008) shows that recovery rate for invader species from low density in general scenarios is contributed by both average fitness-differences between species ξ_i and the overall stabilizing effect A, aka stability of coexistence:

$$\bar{r}_i = \xi_i + A \qquad\qquad 5$$

where the subscript i labels the invader species. The average fitness difference ξ_i is a species level measure on the mean fitness advantage (if it is a positive value) or disadvantage (if it is a negative value) of the invader comparing to the rest of the community. It predicts exclusion in the absence of any stabilizing effect A. In contrast, the stabilizing effect (A) is a community level measure for the overall degree to which coexistence is stabilized in the guild in question. As the ξ_i values average to zero across species, A can be obtained directly by averaging invasion rates over each species in the community as the invader:

$$A = \frac{1}{p}\sum_{i=1}^{p}\overline{r_i} \ . \qquad\qquad 6$$

Thus A has the dual interpretation as 1) the degree of average fitness-inequality between species compatible with coexistence as in Eq. 5, and 2) the average ability of all species in a community to recover from low density in the presence of competitors as in Eq. 6. Under temporal variation, the overall stabilizing effect is mainly contributed by several coexistence mechanisms (Yuan and Chesson, in progress):

$$A \approx \Delta S + \Delta E + \Delta I \ . \qquad\qquad 6$$

The quantity ΔS measures the mean effect of fluctuating size structure. The quantity ΔE measures the mean environmental effect under fluctuating size structure. The storage effect ΔI measure the mean of interaction between environment and competition.

As mentioned, to simplify matters, we consider only symmetric cases where species are identical except their environmental responses. In such cases, the life history differences are minimalized between species. Another fluctuation dependent mechanism, relative nonlinearity ΔN, that arise when species have different nonlinear responses to limiting resources between species, is negligible (Yuan and Chesson In review) and is

omitted from Eq. 6.

In symmetric cases, the quantities ΔS and ΔE both arises with fluctuating structure, unseen in nonstructured model . We find out, through both simulation and approximation, although size structures fluctuate with environment, it is the mean structure differences between invader and resident states matters for coexistence (Appendix). More specifically, mean in size structure will shift more when a species is in invader state than resident state, compared with the equilibrium structure in single species stationary status (Chesson and Yuan, in progress). Both mechanisms ΔS and ΔE are measured directly from simulations (Appendix). The quantify ΔS is measured as the difference in growth rate between invader and resident, with competition and environment fixed at equilibrium, and averaged over fluctuating size structure. This mechanism promote coexistence if size structure shift in direction with demographic advantages. The quantity ΔE is measured as the difference in mean environment effect on growth rate between invader and resident, with competition fixed at equilibrium, averaged over fluctuating environment and size structure. It reflects whether environmental variation enhance the effect of shift in structure. Approximation show it can promote coexistence if shift in structure in structure leads to increasing contribution to population growth on average from the process sensitive to environment (Appendix).

The storage effect ΔI measures the differences between invader and resident in their ability to decouple environment with competition. As a formalization of the concept of temporal niche partitioning, the storage effect is usually the major contributor to the stability of coexistence (Chesson 2003, 2008). Its two prerequisites easily hold up for it to promote coexistence. First, covariance between environment and competition (covEC), which is measured by a formal statistical covariance over time between environment and

competition, must be higher in resident state than in invader state (Appendix, Chesson 2008). Environmental response, such as a seedling germination or potential tree growth, will determines the demand for resources and thus strength of competition. Nevertheless, species will only have a significant effect on competition at resident state, as its density at invader state is negligible. A resident species in favorable environment posts strong self-limitation through intraspecific competition –a high value of covEC. Unless the invader species have the exact same pattern of variation in environmental response as the resident, it has opportunities to escape the competition when the environment favors it but not the resident species –a low value of covEC. The larger the differences in covEC between resident state and the invader state are, the stronger the storage effect gets.

The second critical component of the storage effect is buffered population growth, due to the subadditive (negative) interaction between environment and competition in population growth. As a result, increasing competition does not have such a strong limitation on population growth for a species in unfavorable environment as on species in favorable environment. Buffered population growth arises naturally with forest trees. On one hand, the long life span of trees slow down the population decline in unfavorable environment; on another hand, growth is an irreversible process, biomass accumulated in the tree as it grows and in our model trees cannot decrease in size. The persistence of the population through harsh times means that the benefits accumulated in good environment is not lost completely in bad environment. The stronger the buffer is, the stronger the storage effect is. As buffer is measured by the negative interaction, we flip its sign and put it on natural scale for easier interpretation, the new term defined as the storage coefficient ψ.

In our model, both environmental responses –response in reproduction E_b and

response in individual growth E_g – have an effect on the competition C. Each will generate a covariance between environment and competition (CovEC); both environmental responses interact with the competition to create buffer in population growth (Eq. 3.1, Eq. 3.2). Thus each will contribute to a separate storage effect (Appendix II, III). We are particularly interested in factors that determine the importances of these two storage effects. The two storage effects are measured both directly through simulation (Chesson and Yuan, in progress) and through approximation (Appendix II, III).

Results

In our model coexistence only occur with species-specific responses to environmental variation. Across a wide range of cases, we find that total mechanism magnitude, A, is an increasing linear function of the variances of the environmental responses, var(E_b) and var(E_g), as these are changed proportionally (spp. Fig 1). This means that we can report results simply for fixed values of these variances, which are then always either 0 or 1.

The storage effect

Like the original lottery model, variation in fecundity promotes species coexistence, and the key mechanism is the storage effect (Fig. 3). Also variation in growth does too. For equivalent variances in fecundity and growth, each alone promotes coexistence less strongly than fecundity promotes coexistence alone in the original lottery model. However, together, their combined effect can be as strong or stronger than in the original lottery model (Fig. 3,4). This outcome depends on the correlation within species in fecundity and growth. Positive correlations are strongly synergistic, given a high

coexistence promoting effect. However, with negative correlations these effects

counteract each other, and in some circumstances a strong negative correlation leads to
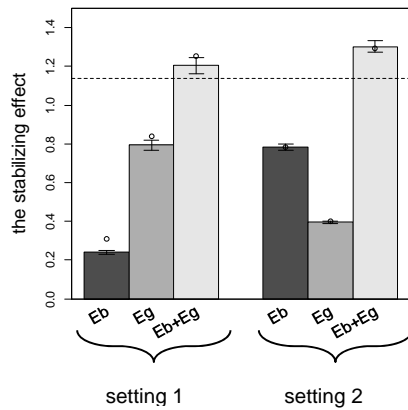
very weak coexistence (Fig. 4).

Figure 3. The stabilizing effects in structured model (bars) compared with mechanisms in unstructured lottery model (dashed line). Storage effect in structured model are plotted as circles. Setting 1 and setting 2 show cases of structured model with contrasts in relative contribution of reproduction and individual growth to population growth. Axis labels: "Eb", "Eg" and "Eb+Eg": structured model respectively with variation in reproduction only, growth only, and both reproduction and growth, respectively. Trees in the non-structured lottery model have the same longevity and fecundity in setting 1of the structured model under single species steady state. Setting 2 have the same mortality schedule with setting 1 but opposite importance of fecundity and growth to population growth. Parameter details are in Appendix I.
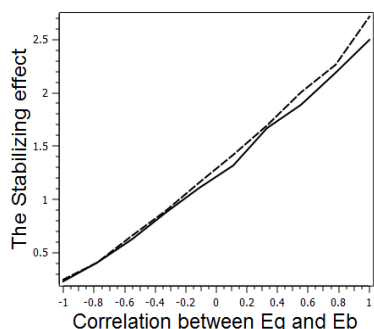
Figure 4. The overall stabilizing effect (solid line) and its main contributor storage effect (dashed line) as the correlation between growth and fecundity increases. Results here are illustrated using the reference demographic schedules: two species have identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. We increase the mean environmental responses, $\mu_b = \mu_g = 3$, so all space can be filled under high correlation to satisfy the lottery assumption. Growth and reproduction have close contribution to average population growth. Mechanisms other than storage effect are negligible. Parameter details are in Appendix I.

These findings can be understood in terms of the approximate formulae for the storage effect (Table 3), which is predominant mechanism in coexistence in this model. Because competition C depends on both growth and reproduction, its covariance with environment response in reproduction E_b, χ_b, involves the covariance between E_b and E_g (environmental response in growth) as well as the variance of E_b. Sensitivities θ of C to E_b and E_g define the dependence of χ_b on this variance and covariance (Table 3, Appendix II). Similarly, χ_g depends on the covariance between E_b and E_g, and variance of E_g. For fixed variances of E_b and E_g, their covariance is proportional to their correlation. Hence, both storage effects, and their sum ΔI_{tot} are increasing functions of the correlation between E_b and E_g. Thus, a strong positive correlation creates a strong synergistic effect between the two storage effects. Conversely, a negative correlation subtracts from each of the separate storage effects making them strongly antagonistic and weakening their total effect (Fig. 4).

Table 3 Functional component of the storage effects

ΔI	Formula	Functional component		
		Storage, on natural scale	θ	covEC χ
ΔI_b	$\psi_b \chi_b$	$\psi_b = \dfrac{\left(p_b + p_{bg}\right) p_s}{1 - p_s}$	$\theta_b = \dfrac{p_b + p_{bg}}{1 - p_s}$	$\chi_b = \theta_b \sigma_{bb} + \theta_g \sigma_{bg}$
ΔI_g	$\psi_g \chi_g$	$\psi_g = \dfrac{\left(p_g + p_{bg}\right) p_s}{1 - p_s}$	$\theta_g = \dfrac{p_g + p_{bg}}{1 - p_s}$	$\chi_g = \theta_g \sigma_{gg} + \theta_b \sigma_{bg}$
ΔI_{tot}	$\psi_b \chi_b + \psi_g \chi_g = \begin{bmatrix} \left(p_{bg} + \overline{p}_{b,g}\right)\left(\chi_b + \chi_g\right) \\ + \left(p_b - \overline{p}_{b,g}\right)\chi_b + \left(p_g - \overline{p}_{b,g}\right)\chi_g \end{bmatrix} p_s$			

Legends: ψ_b storage due to reproduction; ψ_g storage due to growth; $\chi_b = \mathrm{cov}(\mathrm{E_b}, C)$; $\chi_g = \mathrm{cov}(\mathrm{E_g}, C)$; $\sigma_{bg} = \mathrm{cov}(E_b, Eg)$; $\sigma_{bb} = \mathrm{Var}(E_b)$; $\sigma_{gg} = \mathrm{Var}(E_g)$; p_{bg} is proportion of finite growth rate in seedling individual growth; p_g the proportion in sapling growth; p_b the proportion for seedling establishment; p_s the proportion for surviving individuals. $p_b + p_g + p_{bg} + p_s = 1$

Though variation in reproduction and variation in individual growth both lead do storage effect, their importance can be very different (Fig. 3). The importance of the variation in a process is directly proportional to the average fractional contribution of this process to population growth (the value p's) (Table 3). Two critical functional components of the storage effect—sensitivities θ of competition to environmental responses in formulation of covEC, and buffer in population growth measured by storage ψ—can both be simply expressed by the fractional contributions of different life-history stages to population growth (Table 3). Interestingly ψ and covEC depend in very similar ways on these life-history contributions. The odds ratio of the fractional contribution from survival p_s—$p_s /(1 - p_s)$—is a common factor in all ψ's and $1/(1 - p_s)$ is a common factor in all covEC's. Hence the storage is proportional to the odds ratio $p_s /(1 - p_s)$. The remaining terms in the ψ and covEC are $p_b + p_{bg}$ for the recruitment terms, and $p_g + p_{bg}$ for

the individual growth terms. This means that the storage effect from recruitment is enhanced by strong contributions from seedling establishment (p_b) and seedling growth (p_{bg}), while the storage effect from growth is enhanced by strong contributions from sapling growth (p_g), and seedling growth (p_{bg}). Seedling growth is the common element in both storage effects. The relative importance of the two storage effects will therefore be strongly dependent on these growth contributions.

Overall, the contributions of recruitment and growth to the storage effect will be enhanced by having both a strong contribution of that process to growth and strong sensitivity of that process to the environment. Their joint effects are then dependent also on the correlation of E_b and E_g, in other words, the alignment of the environmental sensitivities between reproduction and individual growth. Lurking behind the scenes is persistence of population through survival p_s: without a positive value of p_s there is no buffering and therefore no storage effect.

Given variances and covariances of environmental responses, the fractions p's are all we need to understand the storage effect. Our next question is how do p's depend on the demographic schedules. Because the invader and resident are assumed to have independent responses to the environment, changes in p's between resident and invader do not affect the storage effect: only resident values matters.

The p's summarize complexity in life history by distinguishing the aspects of life history that affect the storage effect and those don't (Fig. 5,6,7). The primary effects that are seen on the p's are life schedule changes that affect the relative performance of seedlings versus growing plants. For instance, seedling size has a big effect on p_b. Increasing $p_b/(1-p_s)$, as a result of the increasing initial seedling size (spp. Fig. 2 Append IV), increase both storage ψ_b, the measure for buffer for bad environment for

reproduction, and θ_b, sensitivity of competition to E_b (Fig. 5). Increasing storage effect in reproduction is contrasted with decreasing storage effect in growth as seedling size increase. As relative contribution from individual growth ($p_g + p_{bg}/(1 - p_s)$) decreases (spp. Fig. 2 Append IV), both ψ_g and θ_g decrease with seedling size (Fig. 5). Changing the relative competitive ability of seedlings and saplings through varying the competitive schedule works similarly (Fig. 7). Increasing competitiveness of seedling to grow leads to increases in $p_{bg}/(1 - p_s)$, as a result favors storage effect in reproduction; yet the overall contribution to individual growth ($p_g + p_{bg}/(1 - p_s)$) are affected minimally, so is the storage effect in growth.

On the other hand, the p's are relatively insensitive to shapes of the mortality and fecundity, and therefore changes in these curves do not affect the storage effect (Figs 6, 7). As mentioned, competitive schedules of growing plants also have minimal effect on the storage effect (Fig 7). However, in some cases we see the mean effect of fluctuating environment ΔE and structure ΔS changing in magnitude as life-history schedules are varied even though the storage effect is not affected (Fig. 6, 7). For instance, as delay in reproduction increases, the p's remain flat, so are the storages. But overall mechanism magnitude changes, as discussed next.

a.   b.

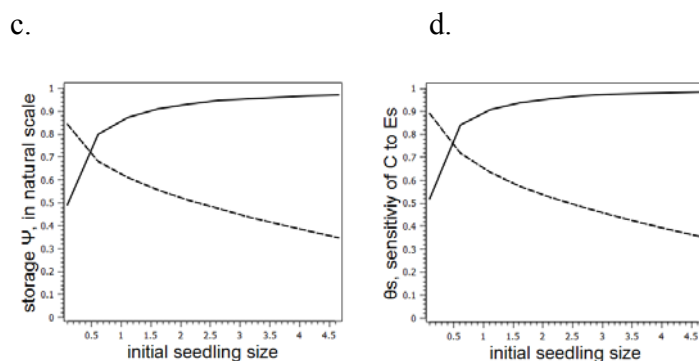c.   d.
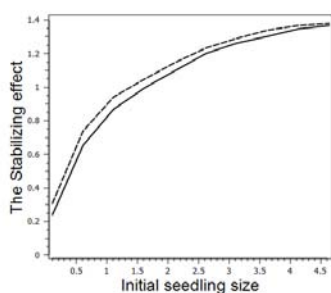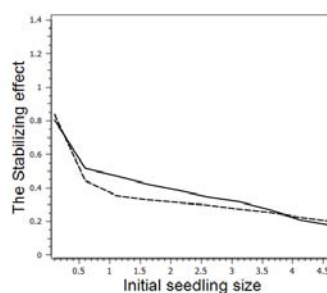
Figure 5. Changes in the overall stabilizing effect, storage effect and its functional components as initial seedling size increase. (a) With only E_b varies, the overall stabilizing effect (solid) and the storage effect (dashed) increase with seedling size. (b) With only E_g varies, the overall stabilizing effect (solid) and the storage effect (dashed) decreases with seedling size. In parallel, storage due to reproduction and θ_b increase with seedling size (solid in c and d respectively); storage due to growth and θ_g decrease with seedling size (dashed in c and d respectively). Results here are illustrated using the demographic schedules where two species have identical delayed linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.

(a) Eb   (b) Eg

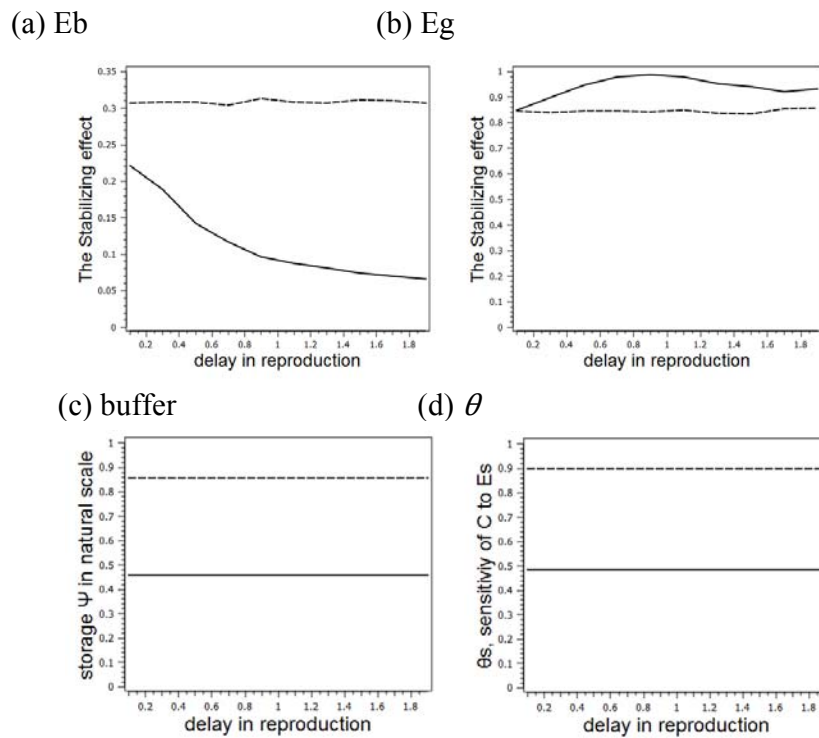(c) buffer   (d) θ

Figure 6. Changes in the overall stabilizing effect, storage effect and its functional components as delay in the reproduction increases. (a) With only E_b varies, the overall stabilizing effect decreases with delay in reproduction. (b) With only E_g varies, the overall stabilizing effect first increases and then decreases with delay in reproduction. The storage effects (dashed line in a,b), and its functional components (c, d) are insensitive to changes in the delay in reproduction. Results here are illustrated using the demographic schedules where two species have identical delayed linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.
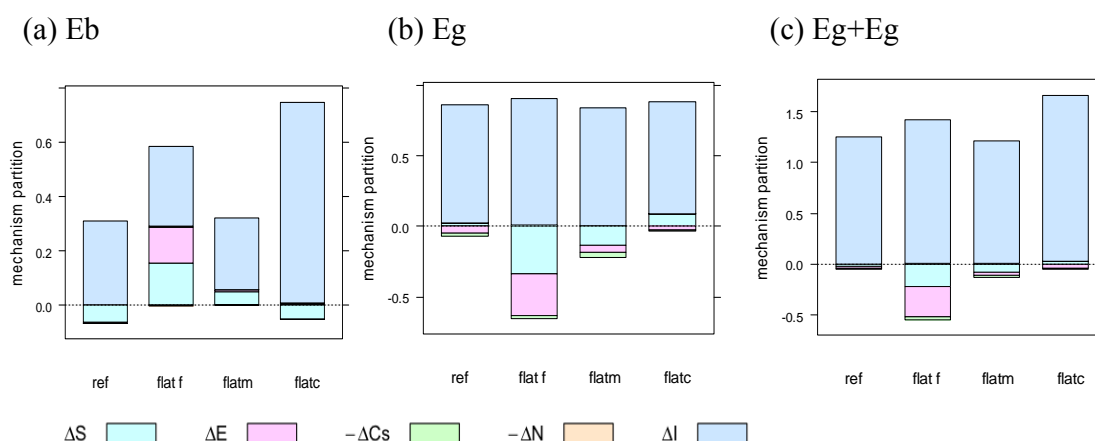
Figure 7. The effect of demographic schedules on the stabilizing effect. In each panel, the dashed line represents the stabilizing effect of the reference case, as already presented in Figure 1. The reference community has two species with identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth (competitive) schedule. In each separate case, one of the schedules is changed to size insensitive one whiles the other two remain the same: "flat f" refers to community with flat fecundity schedule, u-shaped mortality schedule, and hump-shaped growth (competitive) schedule; "flat m" refers to community with flat mortality schedule, linear fecundity schedule and hump-shaped growth (competitive) schedule; "flat c" refers to community with flat competitive schedule, linear fecundity schedule, u-shaped mortality. Between plots comparison are made between (a) community where only reproduction is sensitive to the environment, (b) community where only growth is sensitive to the environment, (c) community where both reproduction and growth are both sensitive to the environment. Parameter details are in Appendix I.

*Mechanisms relating to change in structure between resident and invader (*

ΔE and ΔS)

In this model, nonzero values of ΔE and ΔS require differences in population structure between the resident and invader states. This does not occur in a constant environment because then an invader has the same equilibrium population structure as the resident. With a growing invader population, the relative numbers of juveniles will be higher. However this effect only leads to higher numbers of small individuals when environmental variation is through fecundity variation, not growth (fig 8a). When there is environmental variation in individual growth, the invader cohorts can advance more

rapidly in size leading a shift in invader structure towards larger individuals (fig 8b).
Whether these shifts in structure promote or undermine coexistence, depends on whether
size structure shifted in direction that advantages population growth. For example, the
shift in size distribution to smaller individuals under the reference structure is
disadvantages to population growth because small individuals have low fecundity, high
mortality and low competitive ability. Fig 7a shows this disadvantage is manifested as a
negative contribution from ΔS under the reference fecundity. This disadvantage grows as
fecundity is deferred to larger sizes (fig 6a). With flat fecundity, instead, this
disadvantage is not present, and ΔS may even contribute positively to invader growth (fig
7a). For ΔE, the issue is whether the structure difference between invader and resident
gives greater benefits of the variable environment to the invader. A positive effect from
ΔE is seen in this case with flat fecundity, but not with reference case where small
individuals have low fecundity. In contrast, with variation in growth, flat fecundity leads
to more negative effects compared with the reference, as then there is less benefits to
increases individual size (Fig 7b). When fecundity and growth variation are combined,
the pattern due to growth tends to be dominant. It is important to note, however, that our
reference schedules chosen to be the most realistic among the schedules considered point
to the storage effect as the overwhelmingly dominant mechanism. Flat fecundity gives
the largest values for ΔE and ΔS, but this assumption is not very realistic.

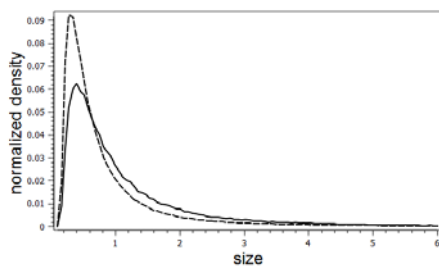(a) Eb only
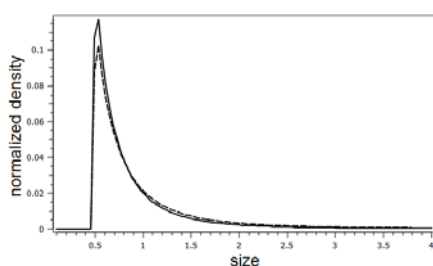
(b) Eg only
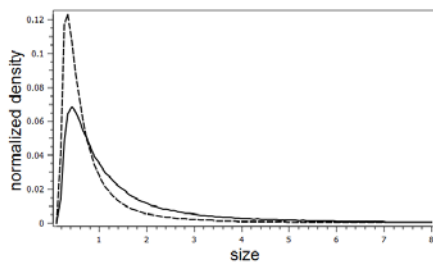
(c) Eb + Eg

Fig 8. Shift in size distributions from resident (dashed) to invader (solid) state. Comparison are made between cases with variation in reproduction only (a), variation in growth only (b), and both reproduction and growth varies (c). Results here are illustrated using the reference demographic schedules: two species have identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.

Discussion

Our cohort-based size-structured lottery model shows that general theory is compatible with studies of interesting biological details. Our model reaffirms the important role of the storage effect in promoting coexistence in a variable environment. Although other mechanisms may be present, for our most realistic combinations of life-history schedules, the storage effect was the major factor for stabilizing coexistence, and sometimes the only significant contributor to coexistence. However, our structured lottery model revealed the potential importance of environmental variation individual growth, which could not be examined in the original unstructured lottery model. Our results show that the key effects of a complex life-history on coexistence through the

storage effect can be summarized by just a few parameters: the fractional contributions to population growth through key processes, principally, fecundity, individual growth and individual survival on average across the structured population. An informative approximation to the magnitude of the storage effect involves only these quantities and the variances and covariances of temporal variation in fecundity and individual growth. This means that the key results understood in relatively simple terms that are only a little more complex than in the unstructured lottery model. This means also that assessing the likely importance of the storage effect in species with complex life histories in nature need not be complex. Details of life-history schedules are not needed, only the relative contributions of key processes to population growth in a population as a whole.

In addition, a structured model allows study of the possible contributions to species coexistence due to changes in the structure as density changes, especially changes between resident and invader states. We found two mechanisms, quantified as ΔS and ΔE, which reflect such shifts. Although normally dominated by the storage effect, these factors can be significant when size shifts between stages that that vary greatly in their contribution to population growth. For example, with flat fecundity and mortality schedules small individuals can contribute more significantly to space recruitment. Shift in structure towards smaller individuals under variation in reproduction leads to strong stabilizing effect through ΔS and ΔE. Shift away from it under variation in growth leads to the opposite. The opposite example is delay in reproduction where sapling contribute nothing to reproduction. Shifting in size structure towards it under variation in growth leads to strong destabilizing effect.

The cohort-based size-structured lottery model that forms the basis for this theory of complex natural system is conceptually simple and easily tractable. Its novelties lie in

many aspects. The model captures detailed processes in seedling recruitment and post-recruitment growths. Species are capable of partitioning the environment during both process. The model is in discrete-time, which is potentially better match than continuous time differential equation models to field studies where observations are made at discrete intervals of time. Tree grows continuously in our model as function of environmental and competitive conditions. It thus an advance over the matrix model of Dewi (1997) in which growth occurs as transitions between discrete size classes. Our model is also fundamentally different from the forest simulator models, which focus mostly on forest succession or prediction of dynamics in an applied setting (Botkin et al. 1972, Pacala et al. 1996). Instead, our model provides a unique perspective to link life history diversity with quantifiable coexistence mechanisms.

Size structure and size dependency of life-history parameters have been much studied as a topic in life-history evolution, and for demographic studies of plant populations, without much attention to community dynamics. In the original lottery models, the important life history processes to recruitment as an adult tree all occur within one year. After this year, trees are insensitive to environment and competition in their rest of life. Our study shows without explicitly introducing size structure, it is impossible to match the abstract models with complex dynamics in real forest. The ordinary lottery model overestimate the importance of the storage effect due to reproduction by assuming that seedling stage is the only stage sensitive to both environment and competition. Meantime, it ignores the role of variation in growth to promote species coexistence. It will bias our understanding of the relative importances of processes for species coexistence in a real system.

The biggest effect of structure on coexistence occurs when stages sensitive to the environment are also sensitive to competition. In the model, variation in seedling recruitment and variation in tree growth lead to distinct storage effects: the storage effect in reproduction that provides species at low density advantages to recruit more and survive the most vulnerable stage of the life; the storage effect in growth that provides species at low density an advantage to grow faster to become more accessible to resources and more ready for reproduction. Indeed, both seedling recruitment and tree growths can be highly variable due to environment, and both processes draw down the resources (Clark and Clark 1994, Binkley et al. 2010, Pretzsch and Biber 2010).

Variation in reproduction and variation in growth have interactive effects on storage effect if they both present. A strong synergistic effect arises if an environment favors reproduction of a species also favors its growth. If it is the other way around, a strong antagonistic effect will rise. There are evidences for both positive, zero and negative correlation between the responses of seedling recruitment (or fecundity) and growth to the physical environment. Positive correlation can occur when the environment favors carbon gain in general, including both reproduction and growth (Despland and Houle 1997). In another example, no correlation occurs within years because fecundity responses to the environment in a previous year and seed matures the year after pollination (Woodward et al. 1993). For some other species, negative correlation occurs because tree growth and reproduction are stimulated by opposite weather conditions (Knops et al. 2007). Negative correlation is also possible if environmental factors trigger a shift in resource allocation within an individual plant between these two processes. Currently sampling of tree growth, seedling recruitment in tropical forests will likely reveal the kinds of correlations present in the near future.

Aside from the temporal variation, mean the strength of storage effect largely depends on how key processes: fecundity, individual growth and individual survival on average contribute to population growth. Hypothesis of life history tradeoff suggest, due to physiological and allocation constraint, it is unlikely that species have advantages in all processes. Guilds of species invest more in reproduction relative to growth on average will in turn have more resource allocated to reproduction. Such guilds are more likely to experience strong storage effect in reproduction and less in growth. Similarly, guilds of species invest more in growth on average relative to reproduction will likely experience strong storage effect in growth and less in reproduction. Longer survival as the buffer favors both storage effects.

Unlike storage effect being only affected by the population level life history processes, the effect of shift in structure is much affected by size-related within-population differences in demographic processes. Whether shift in structure promote or undermine coexistence depends on whether size structure shift in directions where individuals have more demographic advantage. When being small is in great disadvantage, as in the references case studied especially with large delay in reproduction, shift in structure towards larger individuals driven by variation in growth favors species coexistence. If being small has no such disadvantages, as in flat fecundity cases, shift towards smaller individuals driven by variation in reproduction favors coexistence.

The ability to link complex life history with simple coexistence mechanisms made our model powerful. The uniqueness of our model lies in many other respects. The model is in discrete-time, a potentially better match than continuous time models to observations made at discrete intervals of time. Tree grow continuously, and is thus an advance over

the matrix model of Dewi (1997) in which growth occurs as transitions between discrete size classes. Our model is also different from forest models that focus mostly on forest succession or prediction of dynamics in an applied setting (Botkin et al. 1972, Pacala et al. 1996, Purves et al. 2007). It is worth mention that our model share similar philosophy with Integral projection model (IPM) (Easterling et al. 2000, Ellner and Rees 2006, 2007) in terms of avoiding the arbitrary discretization of the population and facilitating parameter estimation of the smooth demographic schedules. In fact our model can be easily extend into the IPM framework to capture variation between individual of the same sizes in life history processes. But we have not find any effect of the individual level variation on our conclusion but much effect on the computational speed (unpublished work). That we stick with the cohort-based model.

Our model has broad implications for species with complex life histories. For example, in animal communities, body size is also an important trait that scales with metabolism and many other life history traits. Our size structured model can be generalized to study species coexistence in these systems as well. Among all systems, we do see a strong role of our model to facilitate studies long-term studies of forests tree.

Long-term studies in different systems with yearly based diameter and height measurements, combined with dendrometer measurements and tree ring chronology, are critical in revealing temporal pattern of tree growth in response to environment (Enquist and Leffler 2001, Nath et al. 2006, Soliz-Gamboa et al. 2012). Overall, the amount of study on variation in tree growth is disproportional to its potential importance for species coexistence, as our study suggest. Many data on growth is measured on multiple-year intervals but aggregation through years loses information on the variation within the census interval (Clark and Clark 1999, 2001). On the other side, studies on seed trap and

seedling plots reveal ubiquitous spatial and temporal variations in seedling recruitment in different systems as a result of environment and species interaction (Schupp 1990, Connell and Green 2000, Harms et al. 2000, De Steven and Wright 2002, Beckage et al. 2005, Wright et al. 2005, Norden et al. 2007, Metz et al. 2008). Inverse modeling can estimate the seed production from the seed rain mapped, providing better knowledge in size-dependence in reproduction (Muller-Landau et al. 2008). Our theory suggests not only the number of the seedling recruits is important, but also how large its initial size is and how fast it can grow in response to the environment. To get the full picture for species coexistence, studies on seedling recruitment need to be integrated with study on tree growth.

What the long-term demographic studies from forest census won't tell us is the separate role of environment and competition on variation in life history traits. Control experiment can artificially creating resident-invader state for different species (Sears and Chesson 2007) but such experiment can be unrealistic and destructive for long-lived perennial plants. In the next step, proper statistical models need to be developed to link the latent processes in interaction between environment and competition with the observations. The recent advancements of hierarchical Bayesian model make it possible to synthesize observations from different life history processes with multiple underlying processes (Metcalf et al. 2009, Clark et al. 2010). Besides, the model can estimate demographic traits that not directly measurable. Integrating statistical models with the cohort-based size structure models will complete our understandings for the different coexistence mechanisms in the forest system. Such work is yet to be done.

Appendix I Demographic schedules

Fecundity schedule

The fecundity of an individual partly depends on a species specific size-dependent fecundity schedule. The fecundity schedule in this study is specified as linear function of size, a_{jc}, after some size threshold, a_0, as in Fig 2a, according to the formula:

$$k_{a_{jc}} = \max(\kappa_1(a_{jc} - a_0), 0).$$

A.1

The parameter κ_1 is the sensitivity of fecundity to size. The values chosen for κ_1 and a_0 for each case illustrated in this study are listed in Table A.1.

Mortality schedule

Mortality rate of any individual is determined by a species-specific mortality schedule. The mortality schedule in this study is chosen as a u-shaped function, as in Fig 2b, specified by five parameters:

$$m_{a_{jc}} = \frac{m_0 e^{-\alpha_d a_{jc}^2} + m_m e^{-\alpha_d(a_{jc} - a_m)^2} + m_\infty(1 - e^{-\alpha_d a_{jc}^2})}{1 + e^{-\alpha_d(a_{jc} - a_m)^2}}$$

A.2

The parameters m_0, m_m and m_∞ specify that the mortality is near m_0 at small sizes, decreases towards m_m as sizes increases, and increase towards m_∞ as size is very large. The parameter α_d determines how rapid mortality rate moves between these different levels with size. The parameter a_m determines the size after which mortality rate increase with size. The parameters α_d and a_m are fixed in all cases as 0.05 and 5 respectively. The values chosen for m_0, m_m and m_∞ for each case illustrated in this study is listed in Table A.1.

Growth schedule, also called competitiveness schedule

As described in Eq. (5), the potential growth of an individual partially depends on a species-specific growth schedules. In this study we choose a Gompertz-alike function for

growth schedule so that in equilibrium cases, tree size increase slowly when small, faster

when tree gets larger, slows down and stop growing eventually when tree get very large

(Fig. 2c).

The original Gompertz growth function is for differential equation model where the

growth of tree follow the following equation

$$\frac{dy}{dt} = b_0 - b_1 y \qquad \text{A.3}$$

where $y = \ln W$, the logarithm of tree size W. We use W instead of a_j here for tree size to

avoid confusion on the actual methods for tree growth used in our study.

We discretize the Gompertz function by integrated Eq. A.3 and obtain

$$y(t+1) = e^{-b_1} y(t) + \frac{b_0}{b_1}[1 - e^{-b_1}]. \qquad \text{A.4}$$

Therefore tree size increases as

$$W(t) = e^{\frac{b_0}{b_1}\left(1 - e^{-b_1 t}\right)} W(t-1)^{e^{-b_1 t}}. \qquad \text{A.5}$$

and the growth in discrete time is

$$W(t) - W(t) = e^{\frac{b_0}{b_1}\left(1 - e^{-b_1 t}\right)} W(t-1)^{e^{-b_1 t}} - W(t) \qquad \text{A.6}$$

in discrete time. Unlike other model that used Gompertz function for the deterministic

growth process, we use it to describe the potential to grow in equilibrium cases, and the

actual growth further depends on environment and competition.

After the parameter transformation, the hump-shape growth schedule is determined

by the following function with two parameters, truncated below zero:

$$c_{a_{jc}} = \max(\beta_1 a_{jc}^{\beta_0} - a_{jc}, 0). \qquad \text{A.7}$$

where $\beta_0 = \exp(-b_1)$ and $\beta_1 = \exp(\dfrac{b_0}{b_1}(1-\beta_0))$. The parameter β_0 and β_1 determines how

fast the growth potential increase with size before it decreases with it at large sizes. The

values chosen for β_0 and β_1 for each case illustrated in this study is listed in Table A.1.

Comparisons between models with different demographic processes

Most results illustrated in this study involve comparisons between demographic

schedules. Several constraints are applied to make the different demographics schedules

comparable. For comparisons between different fecundity schedules, the averaged

fecundity under single species steady state is fixed between schedules. For comparisons

between different mortality schedules, the longevity under single species steady state is

identical between schedules. For comparison on competitive schedule, the average

competitiveness under single species steady state is identical between schedules. These

averaged values are defined later in details, in Eq A.10, A.11 and A.12 respectively.

The average demographic traits, where the constraints are applied, are calculated by

averages weighted by the stationary age structure. To calculate these age-averaged

demographic traits, it is necessary to obtain the age dependency in demographic

schedules. In equilibrium cases, there is a one-to-one correspondence between age

structure and size structure. We know the demographic trait for individuals at certain age

by first figuring out their size at different ages. Under single species steady state

individual grow at fix rate, and there is a unique projection between the size structure and

the age structure. The size of individual at age x is obtained by iteration through the

following process in single species steady state:

$$a_j(x) = a_j(x-1) + c_{a_j(x-1)} e^{\mu_{gj} - C}$$
$$a_j(x-1) = a_j(x-2) + c_{a_j(x-2)} e^{\mu_{gj} - C}$$
$$\ldots$$
$$a_j(2) = a_j(1) + c_{a_j(1)} e^{\mu_{gj} - C}$$

A.8

$a_j(x)$ is defined as the size of individual at age $\underline{x}$, and the size of individual at age 1

is defined as the size of the initial seedling cohort $a_j(1) = a_{js}$. The variable μ_{gj} is the mean

environmental responses in growth and C is the constant competitive responses in single

species steady state. After knowing their sizes at different ages, we could obtain the age-

structured demographic schedule. For individual of age x from species j, we label its

fecundity rate as $k_j(x)$ where $k_j(x) = k_{a_j(x)}$, its mortality rate as $d_j(x)$ where $d_j(x) = d_{a_j(x)}$,

and its competitiveness as $c_j(x)$ where $c_j(x) = c_{a_j(x)}$.

The probability that an individual of species j survives to age x is l_{jx} where

$l_{jx} = \Pi_{i=1}^{x-1}(1 - d_j(i))$. Due to the fixed growth rate under single species steady state, only

certain sizes are possible, which make the model similar to an age-structured matrix

model. Many well-studied properties of the matrix model can be applied. The stationary

age distribution is

$$\pi_{jx} = \frac{l_j x}{\sum_{x=1}^{\infty} l_x}$$

A.9

The stationary age distribution is used as a weight to calculate average demographic

traits. For the purpose of comparing different fecundity schedules, we fixed the average

fecundity, weighted by the stationary age structure in Eq (A.1), under single species

steady state:

$$\overline{k_j} = e^{\mu_{bj}} \frac{\sum_{x=1}^{\infty} k_{jx}(x) l_{jx}}{\sum_{x=1}^{\infty} l_{jx}} \qquad\qquad \text{A.10}$$

where μ_{bj} is the mean environmental responses in reproduction.

For a fixed $\overline{k_j}$, there is no unique choice of μ_{bj} and $k_j(x)$. To avoid

overparameterization, the $k_j(x)$ and $\overline{k_j}$ are chosen first, μ_{bj} are then fixed and can be

estimated numerically. The parameter details on $k_j(x)$ and $\overline{k_j}$ is in Table A.1. For non-

structured lottery model, the average fecundity is simply as $\overline{k_j} = e^{\mu_{bj}}$.

For the purpose of comparing different mortality schedules, we fixed the average life-

span under single species steady state. The life span for individual in structured

population is estimated as:

$$L_j = \sum_{x=1}^{\infty} l_{jx} \ . \qquad\qquad \text{A.11}$$

For the non-structured lottery model, the life span is simply one over the death rate

$1/d_j$.

For the purpose of comparing different competitiveness schedule, we fixed the

average competitiveness weighted by the stationary age structure under single species

steady state:

$$\overline{c_j} = e^{\mu_{gj}} \frac{\sum_{x=1}^{\infty} c_{jx}(x) l_{jx}}{\sum_{x=1}^{\infty} l_{jx}} \qquad\qquad \text{A.12}$$

Similar with the average life-time fecundity, for fixed $\overline{c}_j$ there is no unique choice of

μ_{gj} and $c_{jx}(x)$. The values for $\overline{c}_j$ and $c_{jx}(x)$ are chosen first and then μ_{gj} are solved by

numerical methods. For the non-structured lottery model, the average competitiveness is

simply $\overline{c}_j = e^{\mu_{gj}}$. However, in non-structured lottery model, the absolute magnitude of this

value has no effect on the species coexistence, only the relative magnitude matters

(Chesson and Warner 1981). Besides, the individuals in the non-structured lottery model

do not grow, so it is not meaningful to compare $\overline{c}$ between structured and non-structured

models.

Parameter setting

Parameters for the model to illustrate the results are listed in Table A.1.

Table A.1. Parameter settings in the model

Cases \ Schedules	Fecundity schedule	Mortality schedule	Competitiveness schedule
Fig. 3 nonstructured model	$k = 1.1253706$	$m = 0.065$	NA
Fig. 3 setting 1, Fig. 4, 5, 7 ref Spp. Fig. 1, 2, 4 ref 5 Ref, 6,7	$a_0 = 0$ $\kappa_1 = 1$ $\overline{k} = 1.125$	$m_0 = 0.1$ $m_m = 0$ $m_\infty = 0.02$	$\beta_0 = 0.819$ $\beta_1 = 1.573$ $c=0.528$
Fig. 6 Spp. Fig. 3	a_0 and κ_1 varies $\overline{k} = 1.125$		
Fig. 7 Flat f	$k = 1.125$		
Fig. 7 Flat m		$m = 0.065$	
Fig. 7 Flat c	$a_0 = 0$ $\kappa_1 = 1$ $\overline{k} = 1.125$	$m_0 = 0.1$ $m_m = 0$ $m_\infty = 0.02$	$c=0.528$

Apendix II Approximation for the Storage Effects and CovEC

The storage effects can be measured exactly through simulation, or studied analytically through approximation. We have placed the responsibility in introducing the exact storage effects and the detailed approaches to measure it in our paralleling manuscript Chesson and Yuan (in Progress). The exact storage effect approach facilitates the quantification of coexistence mechanisms in complex models. The results on storage effect shown in main text are the exact values. Nonetheless, to fundamentally understand how life history details affect the storage effect, it is necessary to study each functional component of the storage effects – sub-additivity and covEC – based on the quadratic approximation. As explained in the main text, the strength of the storage effect is proportion to these two components: sub-additivities provide a buffer for population growth in bad environment; invader-resident covariance differences provide invader species advantages to escape the competition. These qualitative descriptions in invader-resident state comparison can be quantified by the following formulae where the community average storage effect due to variation in reproduction is approximated as

$$\overline{\Delta I_b} = \frac{1}{n} \sum_{j=1}^{n} \frac{\gamma_{bj}}{\beta_j} \left(\overline{\chi_{bj}^{-j}} - \overline{\chi_{bj}^{-i}}^{i \neq j} \right), \qquad \text{A.13}$$

and the community average storage effect due to variation in growth is approximated as

$$\overline{\Delta I_g} = \frac{1}{n} \sum_{j=1}^{n} \frac{\gamma_{gj}}{\beta_j} \left(\overline{\chi_{gj}^{-j}} - \overline{\chi_{gj}^{-i}}^{i \neq j} \right). \qquad \text{A.14}$$

In Eq. A.13, the quantity χ_{bj}^{-i} represent the covariance between environment response in reproduction and competition, $\text{cov}(E_{bj}, C)$, for species j when species i is the invader. Similarly, in Eq. A.14, the quantitate χ_{gj}^{-i} represent the covariance between environmental

response in growth and competition, $\text{cov}(E_{gj}, C)$, for species j when species i is the

invader. Thus the quantity $\overline{\chi_{bj}^{-j} - \overline{\chi_{bj}^{-i}}^{i \neq j}}$ and $\overline{\chi_{gj}^{-j} - \overline{\chi_{gj}^{-i}}^{i \neq j}}$ measures the differences in the

covariance between a species in the invader states and the species in resident state. Both

$\overline{\Delta I_b}$ and $\overline{\Delta I_g}$ are averages of the covariance differences for each species in the

community between the two states times the subaddtivity γ, scaled by sensitivity of

competition β.

The quantity γ_{bj}^{-i} measures the interaction between environment in reproduction and

competition for species j and γ_{gj}^{-i} measures the interaction between environment in

growth and competition. The interaction is another important component for storage

effect, different from the covariances. The interaction, in this case as subadditivity,

buffers the population dynamics. It makes sure advantages accumulated in good years for

an invader do not cancel out by population decline in bad years. The estimation of

subadditivity for the cohort-based size structure model is described in details in Appendix

IV. The quantity β_j^{-i} is a scaling factor in time for convenient of comparison between

species with different life history, measured as the sensitivity of growth rate in

competition for species j. The scaling factor β_j^{-i} also partially reflects the longevity of

trees in the forest. Divided by it, we are now compare population growth rate on the unit

of life time rather than per unit of time. In our studies, species have identical mean life

history, and scaling factor is less important.

As shown above, the approximation for the storage effect is essential for

understanding, even though it is less accurate than the exact measure. The quadratic

approximation to get Eq. A.13 and Eq. A.14 has been demonstrated in general models

with single environmental response (Chesson 1994, 2000, 2008) and multiple

environmental responses (Supporting Information, Angert et al 2009), and is not our

focus here. In the rest of this appendix, we focus on how we studied the critical

component of storage effect, CovEC, in this complex model and in the next appendix we

will focus on the other critical component, buffer in population growth measured as sub-

additivity in interaction between environment and competition.

The covariances χ_{bj}^{-i} and χ_{gj}^{-i} is measured directly from simulation by the statistical

covariance over time between the environmental responses and competitive response of

species j. Further approximations on covEC are critical for understanding how life history

details affect species coexistence through the storage effects. The competitive response as

listed in Table 2, takes the form in the two-species invasive analysis:

$$C = \ln\left(\frac{R}{S}\right) = \ln\left(\frac{\sum_c \left(c_{a_{rc}} e^{E_{gr}}(1-m_{a_{rc}}) + [a_{sr} + c_{a_{sr}} e^{E_{gr}}]c_{sr}k_{a_{rc}} e^{E_{br}}\right)N_{rc}}{\sum_c N_{rc} m_{a_{jr}}}\right) \qquad \text{A.15}$$

where $R = \sum_c \left(c_{a_{rc}} e^{E_{gr}}(1-m_{a_{rc}}) + [a_{sr} + c_{a_{sr}} e^{E_{gr}}]c_{sr}k_{a_{rc}} e^{E_{br}}\right)N_{rc}$ is the requirement for

space, $S = \sum_c N_{rc} m_{a_{rc}}$ is the available space released by death and r indicate the resident

species. The requirement for space R depends on the environmental response in growth

and reproduction. The available space S is a constant function in terms of the

environment responses. Therefore the covariance between environment and competition

is reduced as

$$\text{cov}(E,C) = \text{cov}(E,\ln(R)) - \text{cov}(E,\ln(S)) = \text{cov}(E,\ln(R)) \qquad \text{A.16}$$

where E is either E_g or E_b.

As in Table 3, the effect of life history schedules on covEC can be summarized by θ's, the sensitivity of competition to environmental responses. Covariance between environmental responses in reproduction and competition for the resident is:

$$\mathrm{cov}\left(E_{br},C\right)\approx\theta_g\,\mathrm{cov}\left(E_{br},E_{gr}\right)+\theta_b\,\mathrm{var}\left(E_{br}\right) \qquad\text{A.17}$$

and for the invader is:

$$\mathrm{cov}(E_{bi},C)=\theta_g\,\mathrm{cov}\left(E_{bi},E_{gr}\right)+\theta_b\,\mathrm{cov}\left(E_{bi},E_{br}\right). \qquad\text{A.18}$$

Covariance between environmental responses in growth and competition for the resident is:

$$\mathrm{cov}\left(E_{gr},C\right)\approx\theta_g\,\mathrm{var}\left(E_{gr}\right)+\theta_b\,\mathrm{cov}\left(E_{gr},E_{br}\right) \qquad\text{A.19}$$

and for the invader is:

$$\mathrm{cov}\left(E_{gi},C\right)\approx\theta_g\mathrm{cov}\left(E_{gi},E_{gr}\right)+\theta_b\mathrm{cov}\left(E_{gi},E_{br}\right). \qquad\text{A.20}$$

The first step to get the above approximation of covEC is doing linear expansion of ln (R) at the equilibrium value of $E_{gr}=\mu_{gr}$ and $E_{br}=\mu_{br}$. Let $\ln R=f(E_{gr},E_{br})$, and in linear approximation

$$f(E_{gr},E_{br})=f(\mu_{gr},\mu_{br})+f_{E_{gr}}(\mu_{gr},\mu_{br})(E_{gr}-\mu_{gr})+f_{E_{br}}(\mu_{gr},\mu_{br})(E_{br}-\mu_{br})$$
$$+\text{ higher-order term} \qquad\text{A.21}$$

and

$$\theta_0=f(\mu_{gr},\mu_{br})=\ln\left(\sum_c[c_{a_{rc}}e^{\mu_{gr}}\left(1-m_{a_{rc}}\right)+(a_{sr}+c_{a_{sr}}e^{\mu_{gr}})c_{sr}k_{a_{rc}}e^{\mu_{br}}]N_{rc}\right)$$

$$\theta_g=f_{E_{gr}}(\mu_{gr},\mu_{br})=\dfrac{\sum_c(c_{a_{rc}}e^{\mu_{gr}}\left(1-m_{a_{rc}}\right)+c_{a_{sr}}e^{\mu_{gr}}c_{sr}k_{a_{rc}}e^{\mu_{br}})N_{rc}}{\sum_c(c_{a_{rc}}e^{\mu_{gr}}(1-m_{a_{rc}})+(a_{a_{sr}}+c_{a_{sr}}e^{\mu_{gr}})c_{sr}k_{a_{rc}}e^{\mu_{br}})N_{rc}} \qquad\text{A.22}$$

$$\theta_b=f_{E_{br}}(\mu_{gr},\mu_{br})=\dfrac{\sum_c(a_{sr}+c_{a_{sr}}e^{\mu_{gr}})c_{rs}k_{rc}e^{\mu_{br}}N_{rc}}{\sum_c(c_{a_{rc}}e^{\mu_{gr}}(1-m_{a_{rc}})+(a_{a_{sr}}+c_{a_{sr}}e^{\mu_{gr}})c_{sr}k_{a_{rc}}e^{\mu_{br}})N_{rc}}$$

where the term labeled θ_0, θ_g and θ_s are all constant function of the environmental

responses E_{gr} and E_{br}. Replacing the constant function θ_0, θ_g and θ_s into the Eq. A. 21,

the linear approximation of the $\ln R$ is:

$$\ln R \approx \underbrace{\theta_0 + \theta_g \mu_{gr} - \theta_b \mu_{br}}_{\text{constant function of the } E_{gr} \text{ and } E_{br}} + \theta_g E_{gr} + \theta_b E_{br}. \qquad \text{A.23}$$

Taking the above approximation of $\ln R$ into the covEC expression A.16, the first

term in Eq. A. 23 as a constant function of the environmental responses will drops out

when covariance is calculated. We are left with covEC simply be expressed as function

of θ's as well as the variance and covariance of environmental responses in Eq. A.17-

A20.

As we work on the special cases where different species are independent in their

responses to environment, invader species have zero covariances between their

environmental responses and their competitive responses: $\text{cov}(E_{bi}, C) = 0$ and

$\text{cov}(E_{gi}, C) = 0$.

As shown in Eq. A.22, the sensitivity θ_g and θ_b is the average proportional

contribution of the growth (including both adults and seedlings growth) and seedling

recruitment (establishment and growth) to the overall space recruitment respectively. We

can express these two terms using fractional contribution of different component to

population growth, the p's. The finite rate of increase G_j are additively sum of

contributions from survival (G_{sj}), growth of the survived individuals (G_{gj}), seedling

establishment (G_{bj}) and growth of established seedling (G_{bgj}), details in Table A.2.

Correspondingly, fractional contributions p's is defined as the ratio of each contribution

to the finite rate of increase: $p_{sj}=G_{sj}/G$, $p_{gj}=G_{gj}/G$, $p_{bj}=G_{bj}/G$ and $p_{bgj}=G_{bgj}/G$.

Rearrangement in A.22 leads to expression of θ's in p's of species in resident status:

$$\theta_b = \frac{p_{br} + p_{bgr}}{1 - p_{sr}}$$ A.24

and

$$\theta_g = \frac{p_{gr} + p_{bgr}}{1 - p_{sr}} .$$ A.25

Table A 2. Finite rate of increases and its different components

contribution to growth rate,	Formula
Finite rate of increase G_j	$$G_j = \frac{\sum_c \left([a_{jc} + c_{a_{jc}} e^{E_{gi}-C}] s_{a_{jc}} + ([a_{js} + c_{a_{js}} e^{E_{gi}}] c_{js} k_{a_{jc}} e^{E_{bj}-C}) \right)}{\sum_c a_{jc} N_{jc}}$$ $$= G_{sj} + G_{tgj} + G_{bj} + G_{sgj}$$
Survival component G_{sj}	$$G_{sj} = \frac{\sum_c a_{jc} s_{a_{jc}} N_{jc}}{\sum_c a_{jc} N_{jc}}$$
Tree growth component G_{tgj}	$$G_{tgj} = \frac{\sum_c c_{a_{jc}} e^{E_{gi}-C} s_{a_{jc}} N_{jc}}{\sum_c a_{jc} N_{jc}}$$
Seedling establishment component G_{bj}	$$G_{bj} = \frac{\sum_c a_{js} c_{js} k_{a_{jc}} e^{E_{bj}-C} N_{jc}}{\sum_c a_{jc} N_{jc}}$$
Seedling growth component G_{tgj}	$$G_{sgj} = \frac{\sum_c c_{a_{js}} e^{E_{gi}} c_{js} k_{a_{jc}} e^{E_{bj}-C} N_{jc}}{\sum_c a_{jc} N_{jc}}$$

Appendix III Buffering (subadditivity) in the model

The storage effect requires buffered population growth. This is measured the

interaction between the response to the environment and response to competition, as the

quantity γ:

$$\gamma = \frac{\partial^2 r}{\partial E \partial C} \, . \qquad \text{A.26}$$

A negative value, i.e. $\gamma < 0$, is called subadditive. A subadditive interaction gives buffered population growth. Henceforce in this appendix, we will refer to buffered population growth as subadditivity. With subadditivity, population growth of a species will suffer less from competition in a bad environment, than in a good environment. The more negative γ is, i.e. the more subadditive, the better the population can persist through bad environment. Therefore, good recruitment in one year is not going to be canceled out by bad recruitment in another year, also commonly known as the storage processes. In our model, there are two environmental responses – one in reproduction E_b and one in tree growth E_g – both will interact with competition. There is one γ arising from the interaction between each of these environmental responses and competition:

$$\gamma_b = \frac{\partial^2 r}{\partial E_b \partial C} \qquad \text{A.27}$$

and

$$\gamma_g = \frac{\partial^2 r}{\partial E_g \partial C} \, . \qquad \text{A.28}$$

In our size-structured model, the population growth rate takes a complicated form, as the Eq. (13) can be extend in detail as:

$$r_j = \ln G_j(\boldsymbol{E}, C) = \ln \frac{\sum_c \left([a_{jc} + c_{a_{jc}} e^{E_{gi}-C}] s_{a_{jc}} + ([a_{js} + c_{a_{js}} e^{E_{gi}}] c_{js} k_{a_{jc}} e^{E_{bj}-C}) \right) N_{jc}}{\sum_c a_{jc} N_{jc}} \qquad \text{A.29}$$

where G_j is the finite rate of growth. To understand how γ_{bc} and γ_{gc} is determine by the life history details in this complicate structure, we need to divide the population growth

into additive classes. In our model, each cohort of the population is divided into the survival, seedling establishment, seedling growth, and tree growth classes. These classes are not real subpopulation. Nonetheless the action of environment and competition is independent within each classes, though overall they are interactive. This method has been proposed by Chesson 1990. Afterwards it has been described in detail and applied in Dewi 1997 to understand the storage effect in complex size-structured models. Here we described it briefly. The main step includes: 1) calculate the contribution of each class to population growth; 2) determines the sensitivities of these contribution to changes in environment, competition, and the interaction between environment and competition, while the latter is deliberately fixed as zero by the way we choose the classes; (3) the overall sub-additivities can be obtained by calculating the means and covariances of these sensitivities over all the classes weighted by their contribution to population growth. Below the mathematical details is outlined.

In the cohort-based size structure model, if environment varies, the size structure of each species in the community will vary. As a result, the contribution of each size class to the population growth rate will vary over time, and so are sub-additivities. For simplification, I estimate sub-additivity in single species steady state, that is with constant environment. As mentioned, the first step to calculate sub-additivity is by dividing the population growth into additive components $G_{cpj}(\boldsymbol{E}, C)$:

$$G_j(\boldsymbol{E}, C) = \sum_c \sum_{p=1}^{4} G_{cpj}(\boldsymbol{E}, C).$$
A.30

We define $q_{cj} = \dfrac{N_{jc}}{\sum\limits_{c} a_{jc} N_{jc}}$. The component $G_{c1j} = a_{jc} s_{a_{jc}} q_{cj}$ is contributed by the survival of cohort c; the component $G_{c2j} = c_{a_{jc}} e^{E_{gj}-C} s_{a_{cj}} q_{cj}$ is contributed by the tree growth of cohort c; the component $G_{c3j} = a_{js} c_{js} k_{a_{jc}} e^{E_{bj}-C} q_{cj}$ is contributed by the establishment of seedlings produced by cohort c; the component $G_{c4j} = c_{a_{js}} c_{js} k_{a_{jc}} e^{E_g+E_b-C} q_c$ is contributed by the growth of seedlings produced by cohort c. The species label j is omitted from now on for notation simplicity. The logarithm of the finite rate of increase contributed by each component of cohort c is:

$$
\begin{aligned}
g_{c1j} &= \ln G_{c1j} = \ln\left(a_{jc} s_{a_{jc}} q_{cj} \right) \\
g_{c2j} &= \ln G_{c2j} = \ln\left(c_{a_{jc}} s_{a_{cj}} q_{cj} \right) + E_{gj} - C \\
g_{c3j} &= \ln G_{c3j} = \ln\left(a_{js} c_{js} k_{a_{jc}} q_{cj} \right) + E_{bj} - C \\
g_{c4j} &= \ln G_{c4j} = \ln c\left({}_{a_{js}} c_{js} k_{a_{jc}} q_c \right) + E_g + E_b - C
\end{aligned}
\qquad \text{A.31}
$$

The sensitivities of each component of growth rate to changes in environment, competition, and the interaction between environment and competition are each calculated following equations below. The sensitivity of growth rate component g_{cp} to environmental response in reproduction is calculated as

$$
\alpha_{bcp} = \frac{\partial g_{cp}}{E_b}
\qquad \text{A.32}
$$

where $g_{cp} = \ln G_{cp}$. The sensitivity of growth rate component g_{cp} to environmental response in growth is calculated as

$$
\alpha_{gcp} = \frac{\partial g_{cp}}{E_g}.
\qquad \text{A.33}
$$

The sensitivity of growth rate component g_{cp} to competitive response is calculated as

$$\beta_{cp} = -\frac{\partial g_{cp}}{C}.$$ A.34

The sensitivity of growth component g_{cp} to the interaction between environmental response in reproduction and competition is calculated as

$$\gamma_{bcp} = \frac{\partial^2 g_{cp}}{\partial E_b \partial C}.$$ A.35

The sensitivity of growth component g_{cp} to the interaction between environmental response growth and competition is calculated as

$$\gamma_{gcp} = \frac{\partial^2 g_{cp}}{\partial E_g \partial C}$$ A.36

The sub-additivity γ_{bcp} and γ_{gcp} are zero for all cases here since the each component is additive. In more details, the growth rate contributed by survival component g_{c1} is neither sensitive to environment nor competition: $\alpha_{bc1} = \alpha_{gc1} = \beta_{c1} = 0$. The growth rate contributed by growth of established individuals c2 is sensitive to environmental response in growth and competition, $\alpha_{gc2} = \beta_{c2} = 1$ and not sensitive to environmental response in birth, $\alpha_{bc2} = 0$. The growth rate contributed by seedling establishment before growth c3 is sensitive to environmental response in birth and competition, $\alpha_{bc3} = \beta_{c3} = 1$, and not sensitive to environmental response in growth, $\alpha_{gc3} = 0$. The growth rate contributed by growth in seedling c4 is sensitive to environmental response in birth and growth, as well as competition, $\alpha_{bc4} = \alpha_{gc4} = \beta_{c4} = 1$.

From Chesson 1990, the sub-additivity is expressed as the difference in the weighted average of γ and the weighted covariance between sensitivity to environment and sensitivity to competition:

$$\gamma_b = \overline{\gamma}_b - \sum_c \sum_{p=1}^{4} (\alpha_{bcp} - \overline{\alpha}_b)(\beta_{bcp} - \overline{\beta}) \frac{G_{cp}}{\sum_c \sum_{p=1}^{4} G_{cp}} \qquad \text{A.37}$$

and

$$\gamma_g = \overline{\gamma}_g - \sum_c \sum_{p=1}^{4} (\alpha_{gcp} - \overline{\alpha}_g)(\beta_{bcp} - \overline{\beta}) \frac{G_{cp}}{\sum_c \sum_{p=1}^{4} G_{cp}} \qquad \text{A.38}$$

where $\overline{\alpha}_b$, $\overline{\alpha}_g$, $\overline{\beta}$, $\overline{\gamma}_b, \overline{\gamma}_g$ are weighted averages respectively.

The weighted averages $\overline{\alpha}_b$ is expressed as

$$\overline{\alpha}_b = \sum_c \sum_{p=1}^{4} \alpha_{bcp} \frac{G_{cp}}{\sum_c \sum_{p=1}^{4} G_{cp}} \qquad \text{A.39}$$

and $\overline{\alpha}_g$, $\overline{\beta}$, $\overline{\gamma}_b, \overline{\gamma}_g$ are expressed in similar forms. Taking the values of $\alpha_{bcp}, \alpha_{gcp}, \beta_{cp}$ $\gamma_{bcp} = 0$ and $\gamma_{gcp} = 0$ into Eq. A.37 and Eq. A.38 we reduces the formulae into

$$\gamma_b = -\sum_c \frac{G_{c3} + G_{c4}}{G} + \sum_c \frac{G_{c3} + G_{c4}}{G} \sum_c \frac{(G_{c2} + G_{c3} + G_{c4})}{G} \qquad \text{A.40}$$

and

$$\gamma_g = -\sum_c \frac{G_{c2} + G_{c4}}{G} + \sum_c \frac{G_{c2} + G_{c4}}{G} \sum_c \frac{(G_{c2} + G_{c3} + G_{c4})}{G} . \qquad \text{A.41}$$

The growth rate components G_{c1}, G_{c2}, G_{c3} and G_{c4} are obtained directly from simulation. As indicated in Eq. A.40 and Eq. A.41, the relative contribution to tree growth rate in component, G_{c2} and seedling establishment G_{c3} determines whether

variation in growth or variation in birth is more important for species coexistence. If G_{c3}

is larger than G_{c2}, γ_b will have a larger magnitude (a smaller negative number), and

variation in birth will lead to stronger coexistence mechanism, and vice versa.
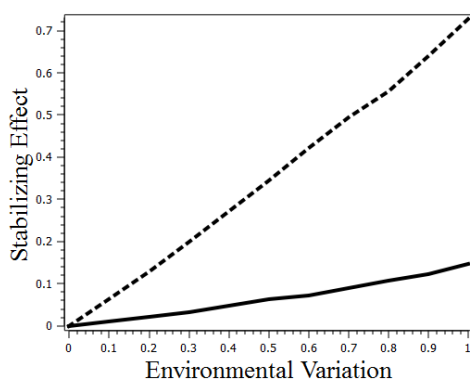
Express in p's, the storages coefficients, which are the positive values measuring the

strength of the subadditivity from A. 40 and A. 41 on natural scale can be simplified as:

$$\psi_{\text{b}} = \frac{\gamma_b}{\beta} = \frac{\left(p_{\text{b}} + p_{\text{bg}}\right)p_{\text{s}}}{1-p_{\text{s}}} \qquad \text{A.42}$$

and

$$\psi_{\text{g}} = -\frac{\gamma_g}{\beta} = \frac{\left(p_{\text{g}} + p_{\text{bg}}\right)p_{\text{s}}}{1-p_{\text{s}}} . \qquad \text{A.43}$$

Appendix IV Supporting results: the effect of life history schedules on the relative

importance of two storage effects.

spp. Fig 1. The stabilizing effect changes proportionally with variation in reproduction (solid line) and variation in growth (dashed line). The solid line represent the case when there is only variation in reproduction; the dashed line represent the case when there is only variation in growth. The structured models have the reference demographic schedules: two species have identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.

(a)

(b)

(c)

(d)
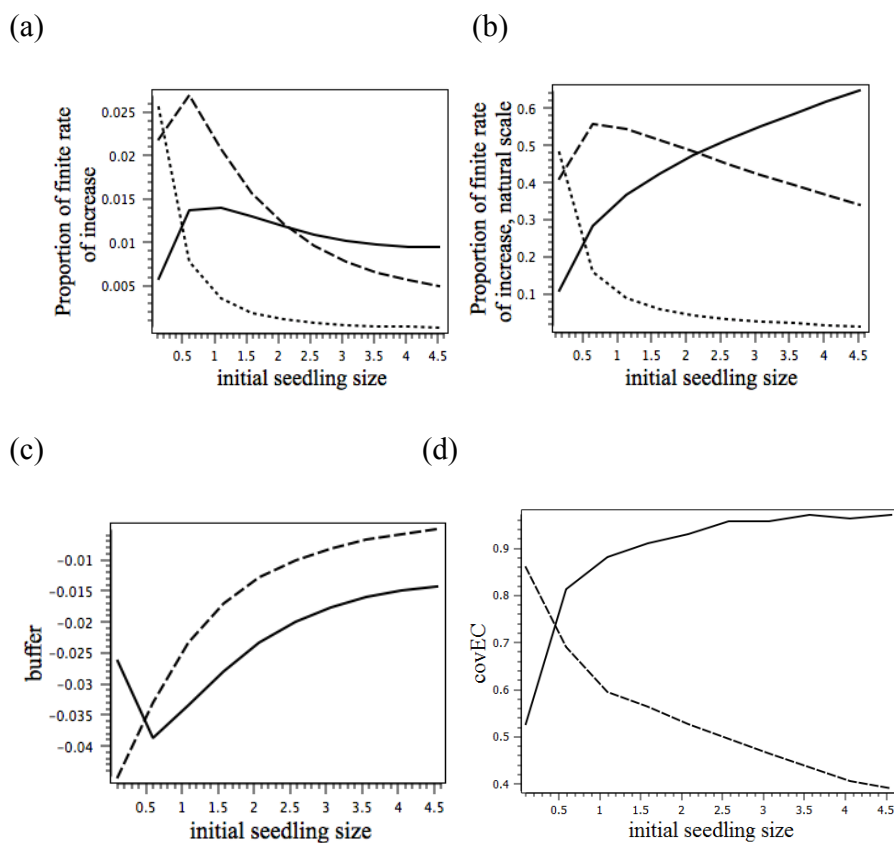
Spp. Fig 2. Shift in resource allocation and functional component of storage effect as initial seedling size increases, for (a) and (b) relative contribution of growth rate are in normal and natural scale: p_b in solid, p_{bg} in dashed and p_g in dotted. Buffer due to reproduction and covEbC are solid in c and d respectively. Buffer due to growth and covEgC are dashed in c and d respectively. The structured models have the reference demographic schedules: two species have identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.

(a)

(b)

(c)

(d)
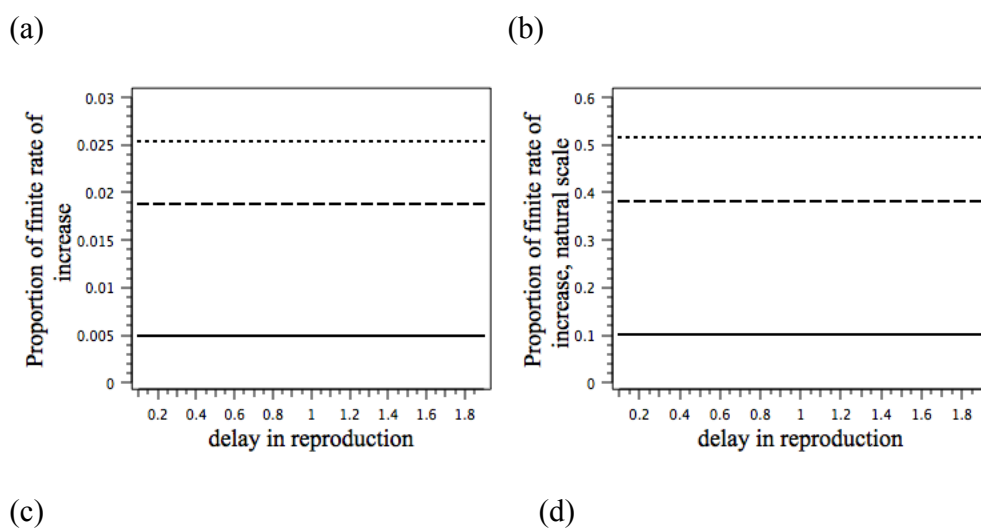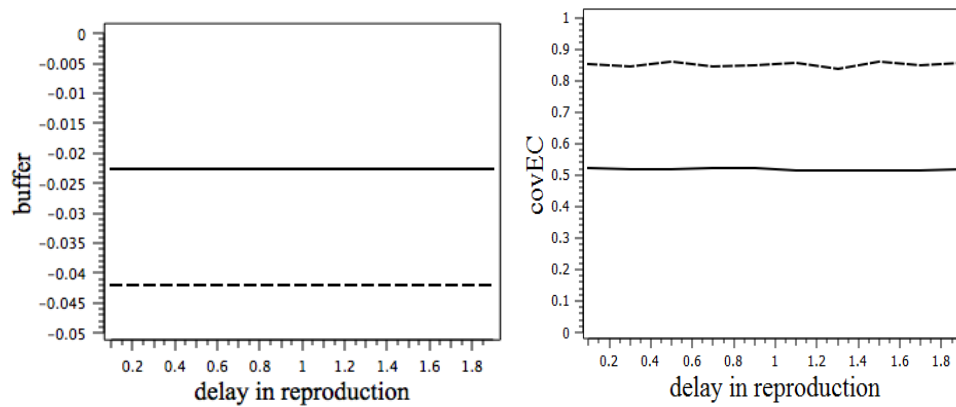
Spp. Fig 3. Shift in resource allocation and functional component of storage effect as delay in reproduction increases, for (a) and (b) relative contribution of growth rate are in normal and natural scale: p_b in solid, p_{bg} in dashed and p_g in dotted. Buffer due to reproduction and covEbC are solid in c and d respectively. Buffer due to growth and covEgC are dashed in c and d respectively. Two species have identical delayed linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.
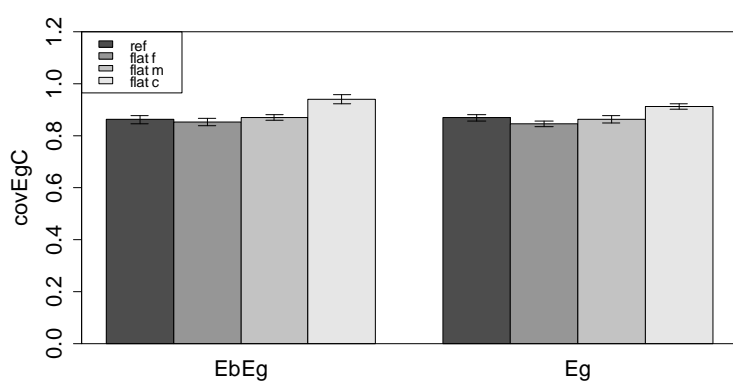
(a)
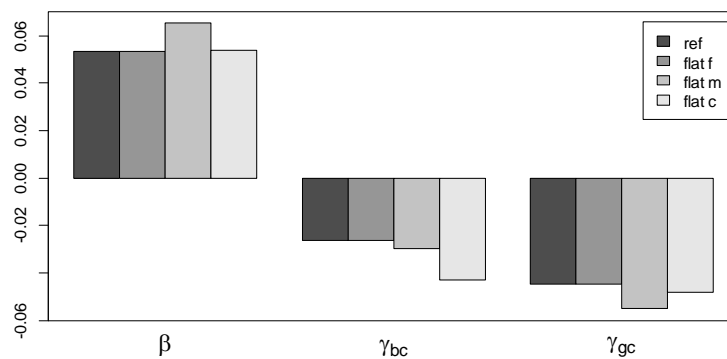
(b)
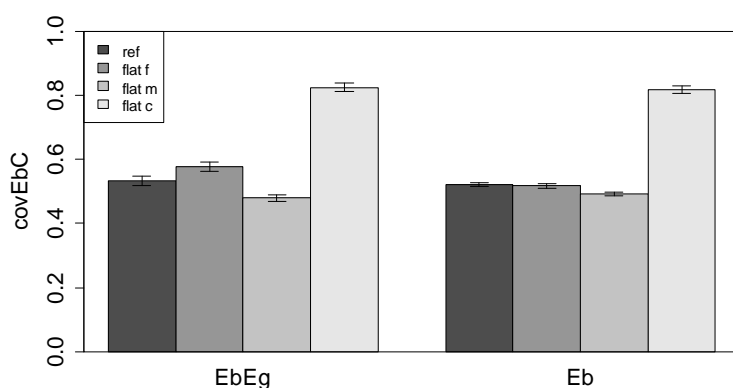
(c)

Spp. Figure 4. The effect of different life history schedules on the components of the storage effect. Panel (a) compares subadditive interactions and scaling factors under different demographic schedules. Panel (b) compares covariance between environmental responses in reproduction E_b and competition C, $\text{cov}(E_b, C)$, under different demographic schedules. The quantity $\text{cov}(E_b, C)$ has similar strength between the case where only E_b varies and the case where both E_b and E_g vary but in independent way. Panel (c) compares covariance between environmental responses in growth E_g and competition C, $\text{cov}(E_g, C)$, under different demographic schedules. The quantity $\text{cov}(E_g, C)$ has similar strength between the case where only E_g varies and the case where both E_b and E_g vary but in independent way. The reference community (ref) has two species with identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth (competitive) schedule. In each separate case, one of the schedules is changed to size insensitive one whiles the other two remain the same: "flat f" refers to community with flat fecundity schedule; "flat m" refers to community with flat mortality schedule; "flat c" refers to community with flat competitive schedule.
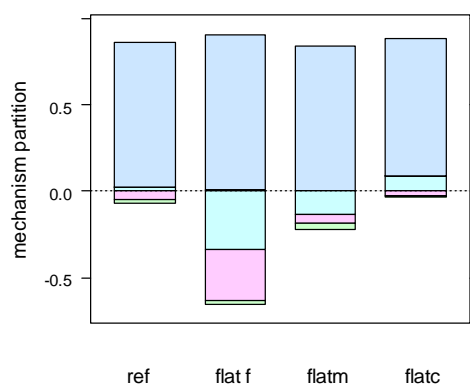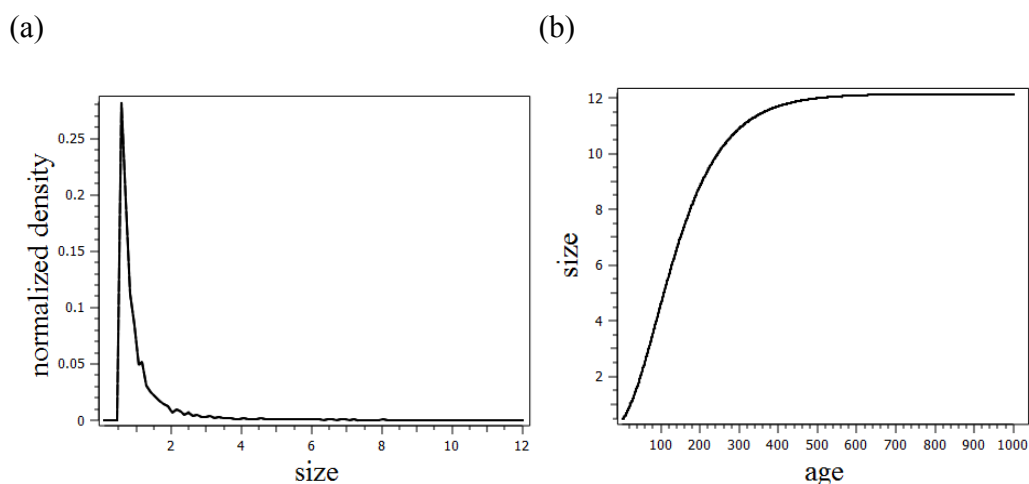
(a) Eb + Eg
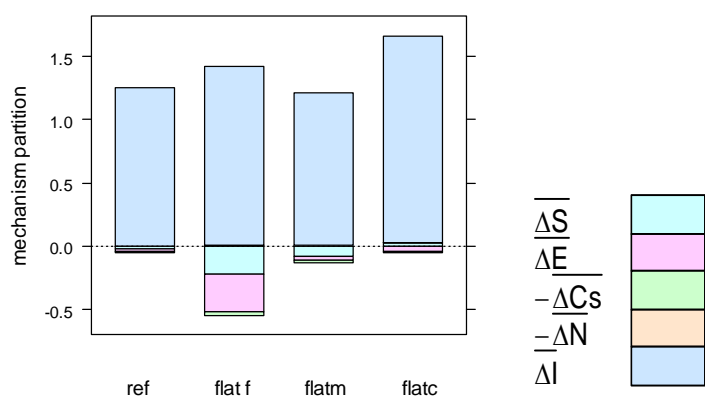
(b) Eb only
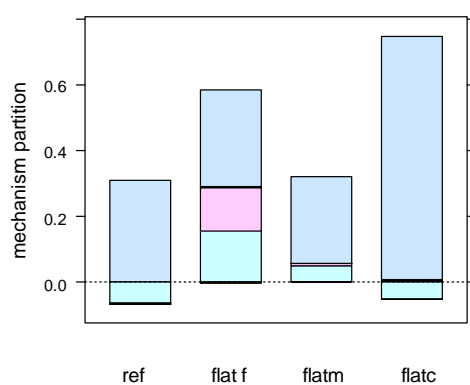
(c) Eg only

Spp. Figure 5. Partition of long-term low density growth rate into different mechanisms. The reference community 'ref' has two species with identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth (competitive) schedule. In each separate case, one

of the schedules is changed to size insensitive one whiles the other two remain the same: "flat f" refers to community with flat fecundity schedule, u-shaped mortality schedule, and hump-shaped growth (competitive) schedule; "flat m" refers to community with flat mortality schedule, linear fecundity schedule and hump-shaped growth (competitive) schedule; "flat c" refers to community with flat competitive schedule, linear fecundity schedule, u-shaped mortality. Between plots comparison are made between (a) community where only reproduction is sensitive to the environment, (b) community where only growth is sensitive to the environment, (c) community where both reproduction and growth are both sensitive to the environment. Parameter details are in Appendix I.

(a)   (b)

Spp. Figure 6 Size distributions and the corresponding age-size relationships in the structured model in constant environment. No invader (solid line) and resident (dashed line overlapped with the solid line of invader) differences in either size structure (a) and age-size relationship exist in constant environment. Results here are illustrated using the reference demographic schedules: two species have identical linear fecundity schedule, u-shaped mortality schedule, and hump-shaped growth schedule. Parameter details are in Appendix I.

a. Eb only   b. Eg only   c. Eb + Eg
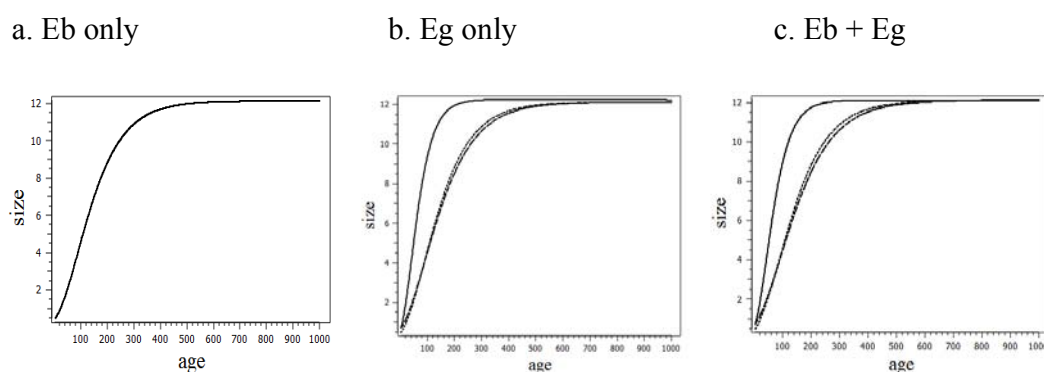
spp. Figure 7. Age size relationship in cases where only Eb varies (a), only Eg varies (b), and both Eb and Eg vary (c). The solid lines represent the invader state, and the dashed lines represent

the resident state. The dotted line in the age-size relationship plots is for the single species stationary status.

References:

Beckage, B., M. Lavine, and J. S. Clark. 2005. Survival of tree seedlings across space and time: estimates from long-term count data. Journal of Ecology **93**:1177-1184.

Binkley, D., J. L. Stape, W. L. Bauerle, and M. G. Ryan. 2010. Explaining growth of individual trees: Light interception and efficiency of light use by Eucalyptus at four sites in Brazil. Forest Ecology and Management **259**:1704-1713.

Botkin, D. B., J. R. Wallis, and J. F. Janak. 1972. SOME ECOLOGICAL CONSEQUENCES OF A COMPUTER MODEL OF FOREST GROWTH. Journal of Ecology **60**:849-&.

Cáceres, C. E. 1997. Temporal variation, dormancy, and coexistence: A field test of the storage effect. Proceedings of the National Academy of Sciences of the United States of America **94**:9171-9175.

Chesson, P. 1982. The stabilizing effect of a random environment. Journal of Mathematical Biology **15**:1-36.

Chesson, P. 1994. Multispecies competition in variable environments. Theoretical population biology **45**:227-276.

Chesson, P., N. J. Huntly, S. H. Roxburgh, M. Pantastico-caldas, and J. M. Facelli. 2013. The storage effect: definition and tests in two plant communities

Temporal Dynamics and Ecological Process. Cambridge University Press.

Chesson, P. and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems The American Naturalist **117**:923-943.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**:343-366.

Chesson, P. L. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical population biology **64**:345-357.

Chesson, P. L. 2008. Quantifying and testing species coexistence mechanisms. Unity in Diversity: Reflections on Ecology after the legacy of ramon margelef.

Clark, D. A. and D. B. Clark. 1992. Life-history diversity of canopy and emergent trees in a neotropical rain-forest. Ecological Monographs **62**:315-344.

Clark, D. A. and D. B. Clark. 1994. Climate-induced annual variation in canopy tree growth in a Costa-Rican tropical rain-forest. Journal of Ecology **82**:865-872.

Clark, D. A. and D. B. Clark. 1999. Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. Ecological Applications **9**:981-997.

Clark, D. A. and D. B. Clark. 2001. Getting to the canopy: Tree height growth in a neotropical rain forest. Ecology **82**:1460-1472.

Clark, J. S., D. Bell, M. Dietze, and M. Hersh. 2010. Models for demography of plant populations. Pages 431-481 *in* O. H. T. and W. M., editors. Handbook of Bayesian Analysis. Oxford Univ. Press, New York.

Comins, H. N. and I. R. Noble. 1985. Dispersal, Variability, and Transient Niches: Species Coexistence in a Uniformly Variable Environment. The American Naturalist **126**:706-723.

Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. Gunatilleke, C. V. S. Gunatilleke, P. Hall, K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. LaFrankie, S. L. de Lao, J. R. Makana, M. N. S. Noor, A. R. Kassim, S. Russo, R. Sukumar, C. Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa, and T. Zillio. 2006. The importance of demographic niches to tree diversity. Science **313**:98-101.

Connell, J. H. and P. T. Green. 2000. Seedling Dynamics over Thirty-Two Years in a Tropical Rain Forest Tree. Ecology **81**:568-584.

Danks, H. V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada (Terrestrial Artropods).

De Steven, D. and S. J. Wright. 2002. Consequences of variable reproduction for seedling recruitment in three neotropical tree species. Ecology **83**:2315-2327.

Despland, E. and G. Houle. 1997. Climate influences on growth and reproduction of Pinus banksiana (Pinaceae) at the limit of the species distribution in eastern North America. American Journal of Botany **84**:928.

Dewi, S. 1997. Structured models of ecological communities in fluctuating environments. The Australian National University.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: Applying a new structured population model. Ecology **81**:694-708.

Ellner, S. P. and M. Rees. 2006. Integral projection models for species with complex demography. American Naturalist **167**:410-428.

Ellner, S. P. and M. Rees. 2007. Stochastic stable population growth in integral projection models: theory and application. Journal of Mathematical Biology **54**:227-256.

Enquist, B. J. and A. J. Leffler. 2001. Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. Journal of Tropical Ecology **17**:41-60.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404**:493-495.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Iida, Y., L. Poorter, F. J. Sterck, A. R. Kassim, M. D. Potts, T. Kubo, and T. Kohyama. 2013. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. Ecology.

King, D. A., S. J. Davies, and N. S. M. Noor. 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. Forest Ecology and Management **223**:152-158.

Knops, J. M. H., W. D. Koenig, and W. J. Carmen. 2007. Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. Proceedings of the National Academy of Sciences **104**:16982-16985.

Metcalf, C. J. E., C. C. Horvitz, S. Tuljapurkar, and D. A. Clark. 2009. A time to grow and a time to die: a new way to analyze the dynamics of size, light, age, and death of tropical trees. Ecology **90**:2766-2778.

Metz, M. R., L. S. Comita, Y. Y. Chen, N. Norden, R. Condit, S. P. Hubbell, I. F. Sun, N. Noor, and S. J. Wright. 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. Journal of Tropical Ecology **24**:9-18.

Muller-Landau, H. C., R. S. Condit, J. Chave, S. C. Thomas, S. A. Bohlman, S. Bunyavejchewin, S. Davies, R. Foster, S. Gunatilleke, N. Gunatilleke, K. E. Harms, T. Hart, S. P. Hubbell, A. Itoh, A. R. Kassim, J. V. LaFrankie, H. S. Lee, E. Losos, J. R. Makana, T. Ohkubo, R. Sukumar, I. F. Sun, N. M. N. Supardi, S. Tan, J. Thompson, R. Valencia, G. V. Munoz, C. Wills, T. Yamakura, G. Chuyong, H. S. Dattaraja, S. Esufali, P. Hall, C. Hernandez, D. Kenfack, S. Kiratiprayoon, H. S. Suresh, D. Thomas, M. I. Vallejo, and P. Ashton. 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecology Letters **9**:575-588.

Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. Journal of Ecology **96**:653-667.

Nath, C. D., H. S. Dattaraja, H. S. Suresh, N. V. Joshi, and R. Sukumar. 2006. Patterns of tree growth in relation to environmental variability in the tropical dry deciduous forest at Mudumalai, southern India. Journal of Biosciences **31**:651-669.

Nehring, S. 1995. Dinoflagellate resting cysts as factors in phytoplankton ecology of the North Sea. Helgoländer Meeresuntersuchungen **49**:375-392.

Norden, N., J. Chave, A. Caubere, P. Chatelet, N. Ferroni, P. M. Forget, and C. Thebaud. 2007. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. Journal of Ecology **95**:507-516.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. Ecological Monographs **66**:1-43.

Pake, C. E. and D. L. Venable. 1996. Seed Banks in Desert Annuals: Implications for Persistence and Coexistence in Variable Environments. Ecology **77**:1427-1435.

Palmer, M. W. 1994. VARIATION IN SPECIES RICHNESS - TOWARDS A UNIFICATION OF HYPOTHESES. Folia Geobotanica & Phytotaxonomica **29**:511-530.

Pretzsch, H. and P. Biber. 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **40**:370-384.

Purves, D. W., J. W. Lichstein, and S. W. Pacala. 2007. Crown Plasticity and Competition for Canopy Space: A New Spatially Implicit Model Parameterized for 250 North American Tree Species. Plos One **2**.

Schupp, E. W. 1990. ANNUAL VARIATION IN SEEDFALL, POSTDISPERSAL PREDATION, AND RECRUITMENT OF A NEOTROPICAL TREE. Ecology **71**:504-515.

Sears, A. L. W. and P. L. Chesson. 2007. New methods for quantifying the spatial storage effect: An illustration with desert annuals. Ecology **88**:2240-2247.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology & Evolution **19**:605-611.

Soliz-Gamboa, C. C., A. Sandbrink, and P. A. Zuidema. 2012. Diameter Growth of Juvenile Trees after Gap Formation in a Bolivian Rain Forest: Responses are Strongly Species-specific and Size-dependent. Biotropica **44**:312-320.

Soong, K., M.-h. Chen, C.-l. Chen, C.-f. Dai, T.-y. Fan, J.-j. Li, H. Fan, K.-m. Kuo, and H. Hsieh. 2003. Spatial and temporal variation of coral recruitment in Taiwan. Coral Reefs **22**:224-228.

Thomas, S. C. 1996. Relative size at onset of maturity in rain forest trees: A comparative analysis of 37 Malaysian species. Oikos **76**:145-154.

Turelli, M. 1981. Niche overlap and invasion of competitors in random environments I: models without demographic stochasticity Theoretical Population Biology **20**:1-56.

Usinowicz, J., S. J. Wright, and A. R. Ives. 2012. Coexistence in tropical forests through asynchronous variation in annual seed production. Ecology **93**:2073-2084.

Venable. 2007. Bet hedging in a guild of desert annuals. Ecology **88**:1086-1090.

Venable, Pake, and Caprio. 1993. Diversity and Coexistence of Sonoran Desert Winter Annuals. Plant Species Biology **8**:207-216.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125-159.

Wright, J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia **130**:1-14.

Wright, S., H. Muller-Landau, O. Calderon, and A. Hernandez. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology **86**:848-860.

Yuan, C. and P. Chesson. In review. The relative importance of relative nonlinearity in the lottery model. Theoretical population biology.

Appendix C

Coexistence of species with contrasting life histories: the role of tradeoffs for diversity maintenance in a variable environment

Chi Yuan[1] and Peter Chesson[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, United States

Corresponding author

C. Yuan: cyuan@email.arizona.edu, Ph: (520) 621-1889

P. Chesson: pchesson@u.arizona.edu, Ph: (520) 621-1451

Abstract

Complex life histories potentially carry much information about species differences in ecological strategies. Identifying which aspects of these differences affect species coexistence is a critical task for theory. Formulating differences in mean demographic rates between species as tradeoffs, we ask whether such tradeoff lead to stabilizing effect alone or modify other stabilizing mechanisms. Using a continuous-size structured lottery model, we are able to study both tradeoffs in relative importances between reproduction and individual growth, and tradeoffs in size-dependency of these life history processes. We demonstrate that quantifying coexistence mechanisms is essentially no more difficult for species with complex life histories than for species with simple life histories. In a constant environment, life-history tradeoffs can only affect average fitness-differences between species, and potentially act as equalizing mechanisms. In variable environment, tradeoff further leads to equalizing effect of fluctuation dependent mechanisms. Stable coexistence arises only in a variable environment in our model, but the strength of the stabilizing effect depends on life-history tradeoffs. The storage effect, the main stabilizing mechanism in our model, is strongest when the sensitivity of a life-history process to variation in the environment is aligned positively with the tradeoff in mean importance between life-history processes. Thus, a species with high environmental sensitivity in fecundity should have an average advantage in fecundity relative to a species with high sensitivity in individual growth, which should have an advantage in individual growth. Size-dependency in demographic rates can affect species

coexistence through changes in mean structure with population density. For a, stabilizing effect to occur for two species from opposite size-dependency in life history processes, opposite shifts in size structure are needed. However, an appreciable stabilizing effect occurs only under very restrictive circumstances.

Introduction

Every species is unique and there is wide variation in life history strategies (Stearns 1992). There have been many attempts to categorize species into functional groups based on their life histories, but detailed studies within groups invariably reveal finer differences in life-history (Clark and Clark 1992). Striking species-specific recruitment, individual growth and survival patterns are commonly observed. It is widely believed that such diversity in demographic traits and their patterns of ontogeny can promote species coexistence (Lusk and Smith 1998, Nakashizuka 2001, Kneitel and Chase 2004, Gilbert et al. 2006, Wright et al. 2010). But questions arise: are differences in different aspects of life history strategies between species equally important for species coexistence? What are the specific coexistence mechanisms involved? Identifying which aspects of the differences matter for species coexistence is critical for understanding the maintenance of species diversity.

Our previous work studied a community model with continuous size structure that allows the formulation of detailed life history strategies. In the model, species' recruitment rates and individual growth rates could be sensitive to variation over time in the physical environment in species-specific ways. However, we had assumed species

have identical mean life history. It is the purpose of this paper to examine the effects of contrasting differences in size dependence of vital rates between species on their coexistence. We seek to understand whether species differences in this dependence alone can act as coexistence mechanisms through trade-offs between species in their life-history schedules, and how these life-history schedule differences interact with the mechanisms previously elucidated.

In a size-structured community model, two forms of the storage-effect coexistence mechanism can arise, one from variation in recruitment, and the other from variation in individual growth. Both mechanisms are affected by the population stage structure. This previous work (Appendix B) also showed that another mechanism could arise under some circumstances due to density-dependence of size structure, but only in a variable environment when the storage effect would also be present.

Species differences in life history traits might affect coexistence in two different ways. They might affect average fitness differences, which would not alone lead to stable existence. On the other hand they might lead to or affect stabilizing mechanisms, which by definition are necessary for stable coexistence (Chesson 2000). Such mechanisms enhance a species' ability to recover from low density (Chesson 2000). Stabilizing mechanisms can be seen to work by enhancing intraspecific density dependence relative to interspecific density dependence on some spatial or temporal scale.

There has been much interest in species differences in mean demographic rates, formulated as tradeoffs, in studies about life history evolution and population

demography. While it is commonly believed that such trade-offs are maintained by inherent differences in species' adaptation to the environment, their consequences for species coexistence are not clear. Demographic tradeoffs such as growth-mortality, growth-fecundity, and propagule size-number between species have been widely observed in nature (Jakobsson and Eriksson 2000, Gilbert et al. 2006, Wright et al. 2010, McMahon et al. 2011). There is the potential that different positions on a tradeoff curve may have advantages under different circumstances. For example, in forests, it is hypothesized that trees with an advantage in individual growth can do better in high light while trees with advantages in survival can do better in low light (Kobe 1999). It is common to see it assumed that life history tradeoffs promote species coexistence, but some people question their sufficiency to support high species diversity (Condit et al. 2006, Esther et al. 2011). The basic issue is that mere demonstration of life-history differences between coexisting species is not sufficient to say that they have a role in coexistence. There need to be serious studies to investigate whether such mean differences affect average fitness differences or stabilizing mechanisms (Chesson 2000).

Tradeoffs in demographic rates can easily be seen to have a role in equalizing average fitness differences between species (Hubbell 2001, Turnbull et al. 2008, Ostling 2012). For example, trees with higher relative growth rates usually have higher mortality rates due to physiological constraints such as low wood density (Iida et al. 2011, Iida et al. 2013). Producing a larger number of offspring often sacrifices the quality of each individual (Turnbull et al. 1999, Jakobsson and Eriksson 2000). However, it is now known theoretically that the existence of such tradeoffs, although tending to equalize average performance of different species, need not stabilize coexistence (Chesson 2000).

Nonetheless, quantifying these equalizing effects is critical. Similar average fitnesses between species make stable coexistence easier if stabilizing mechanisms are present. It seems less clear how stabilizing mechanisms can arise from tradeoff in mean demographic rates.

Apart from the unknown effects of differences in mean demographic rates, it is known that differences in responses of life-history traits to temporal environmental variation can lead to stable coexistence by the storage effect. Underlying physiology differences between species determine differences in their resource use efficiencies. In desert annual plants, for example, opposite patterns of temperature and rainfall can favor germination and growth in different species (Kimball et al. 2012, Chesson et al. 2013). A favorable physiological response to environmental conditions, however, can be associated with stronger competition if many individuals respond at the same time, and so draw down resources. Thus, a species at high density in a favorable environment can contribute strongly to competition and so experience stronger self-limitation. Thus, there is positive covariance between environmental responses and competition (covEC). In contrast, a species at low density has more opportunities to escape competition and take advantage of a good environment if other species do not respond favorably to the same conditions. Thus, it might have only a weak positive covariance between its environmental response and competition, or negative covariance. These differences between high and low density are at the heart of the storage effect coexistence mechanism, but it is not known how they are affected by tradeoffs in life-history schedules.

Given the importance of the storage effect in our previous study where species had the same size-dependence of their life-history schedules, we are particularly interested to see how differences between species in these life-history schedules might interact with this mechanism. This question is especially important given our finding that the strength of storage effect is highly dependent on the mean life-history properties. In addition, whether density-dependence of size structure promotes or undermines coexistence depends highly on the size-dependency of life history schedules.

In this study we ask two main questions. First, do tradeoffs in mean demographic rates and the size dependence of demographic rates lead to stabilizing effects alone? Second, do these tradeoffs interact with mechanisms that depend on fluctuations over time in demographic rates to affect coexistence? We seek the answers by quantifying coexistence mechanisms, and seeing how the magnitudes of the mechanisms change with life-history differences between species. In a previous study of a nonstructured lottery model we were able to show how a fecundity-mortality tradeoff interacts with environmental variation to increase the strength of relative nonlinearity and weaken the storage effect. In this study, we have the opportunity to examine a different tradeoff that does not arise in the simple lottery model, namely the fecundity-individual growth tradeoff as an example to provide a clear link between life history diversity and species coexistence.

Method

Model description

To study how these complex life histories affect different coexistence mechanisms, we use our recently developed continuous-size structured lottery model. In the model, important traits of species, such as size to maturity, body sizes, ability to grow and reproduce, are all size-dependent. Size explicit traits allow us to capture tradeoffs in mean life history process and how they shift through ontogeny. More importantly, in our model, critical life history processes, i.e. reproduction and individual growth, can be sensitive to both the physical environment and competition. Quantification of coexistence in this model in essence is no more difficult than in the simple lottery model. Theory development (in the next section) summarizes the complexity in life history traits on different coexistence mechanisms.

The model will be illustrated using forest trees. While we used it in previous studies for a guild of species with identical mean life history schedules, two species in this study have different mean life history schedules. Details of the model are described in Yuan and Chesson and Appendix I. Table A.1 in Appendix I gives the notation. The model works in discrete time. In each unit of time, deaths occur and free up space to give total available space $S(t)$ for which the living compete. Demand for space $R(t)$ comes from two sources: recruitment of new individuals, and growth of new and established individuals. Both can vary with the environment. Competition for the space is quantified as a ratio of demand to supply on the log scale:

$$C = \ln\left(\frac{R}{S}\right). \qquad\qquad 1$$

Per capita offspring produced by each cohort depends on a species-specific size-dependent fecundity schedule $k_{j,a_{jc}}$, where a_{jc} is the size of individuals in cohort c of species j, and an environmental response in reproduction E_{jb}. The formula for per

capita offspring is equal to $k_{j,a_{jc}} e^{E_{bj}(t)}$. Each offspring has an initial size a_{sj}, but grows in size depending on the environment and its competitiveness. The growth of an individual, whether seedling or sapling, in general depends on a species-specific size-dependent competitiveness schedule $c_{j,a_{jc}}$ and the environmental response in individual growth E_{jg}. Together these two factors give a net maximum growth amount of $c_{j,a_{cj}} e^{E_{gj}}$, which is then reduced by competition. The environmental response in reproduction E_{jb} and individual growth E_{jg} are normal random variables with mean μ_{jb}, μ_{jg} and variances $\sigma_{jb}^2, \sigma_{jg}^2$ respectively.

The total potential growth and seedling recruitment lead to a total resource demand $R(t)$ in Eq. (1). It is the sum over space required by each new seedling to establish and grow, and for the growth of each surviving sapling and adult. Competition modifies the actual area of offspring recruited to $k_{j,a_{jc}} e^{E_{bj}-C}$ and actual growth of established individuals to $c_{j,a_{cj}} e^{E_{gj}-C}$. The allocation of space to an individual is proportional to its demand for space divided by competition. We assume the initial growth of offspring do not suffer from competition. Instead, competition restricts the total area they can occupy, and growth has the effect of modifying the actual number recruited for a given area recruited. Using the notation $m_{a_{jc}}$ for mortality, N_{jc} for cohort density, the population growth rate is calculated as the natural log of the ratio of space occupied by the population from one time to another, which equals

$$r_j(t) = \ln \frac{\sum_c \left(\left[a_{jc} + c_{j,a_{jc}} e^{E_{gi}-C} \right] \left(1 - m_{a_{jc}} \right) + \left[a_{js} + c_{j,a_{js}} e^{E_{gi}} \right] k_{j,a_{jc}} e^{E_{bj}-C} \right) N_{jc}}{\sum_c a_{jc} N_{jc}}, \qquad (2)$$

where the sums are over cohorts. In Eq. (2), time, t, is omitted from the E's, C, and N_{jc} for notational simplicity.

We will further scale growth rate by dividing Eq. (2) with β_j, the sensitivity of the growth rate to competition

$$\beta_j = -\frac{\partial r_j}{\partial C} \, , \tag{3}$$

which we evaluate in a constant environment at equilibrium (Yuan and Chesson, in progress). The quantity $1/\beta_j$ has units of time defines a timescale that we call the natural scale: the timescale of responsiveness to competition. Past work has shown that expressing population growth on the natural scale provides more effective comparisons between species with contrasting life history (Chesson 2008).

The size structure is defined as a set $S_j = \left\{ \begin{bmatrix} a_{jc} \\ N_{jc} \end{bmatrix}, c = 1, 2... \right\}$ that describes the fraction of the population of certain sizes. The population growth rate in Eq. (2) can be expressed as a function (G and its ln form g) of environment, competition and structure:

$$r_j = g(\mathbf{E}_j, C, S_j) = \ln G_j(\mathbf{E}_j, C, S_j). \tag{4}$$

We use invasibility as our definition of species coexistence. The strength of coexistence is quantified using the rate at which a species recovers after perturbed to low density, while its competitor that has converged on stationary fluctuations (Turelli 1981, Chesson 1994). The species held at lower density is called the invader species, and we define its recovery rate by measuring the long-term low density growth rate $\bar{r_i}$ by:

$$\overline{r_i} = \frac{\lim\limits_{t' \to \infty} \sum\limits_{t=1}^{t'} r_i(t)}{t'} \qquad (5)$$

We make the assumption, which is borne out by simulations, that the fluctuations over time in a single species community converge on a stationary stochastic process given independent and identically distributed fluctuations in the environment over time. A single species in this state is called the resident species in an invasibility analysis. Coexistence is stable when both species have a positive recovery rate in invader state.

We first ask whether differences in life history schedules lead to stable coexistence in a constant environment in our model. We then ask how mean differences in life history interact with variation in life history by looking at cases where environmental variation acts on different life history processes: reproduction, individual growth, or both. In addition to our main approach to partitioning recover rate into different contributes of coexistence mechanisms (in the next section), we measure the coexistence region by the average fitness differences of two species that allow mutual invasion. Among many ways to vary average fitness, we vary the difference in mean environmental response in reproduction between species (μ_{b1}-μ_{b2}) while fixing the other parameters. The range of μ_{b1}-μ_{b2} that allows successful mutual invasion is a measure of the region of stable coexistence.

Theory development

Thee recovery rate $\overline{r_i}$ can be partitioned into different coexistence mechanisms:

$$\overline{r_i} \approx \overline{r_i}' + \Delta S_i + \Delta E_i + \Delta I_i . \qquad (6)$$

The individual coexistence mechanisms in Eq (6) are species specific indicated by *i* due to asymmetry in mean life history schedules. Each mechanism measures different aspects of the effects of life history through an invader-resident comparison (Chesson 1994). All mechanisms are measured directly from simulations. The approximations are used to facilitate understanding. The first term $\bar{r}_i'$ measures contribution due to average fitness differences and fluctuation independent mechanisms—mechanisms in shorter time scale than unit of time considered. The quantity $\bar{r}_i'$ is thus measured as invader-residence difference in the recovery rate at equilibrium. Three fluctuation dependent mechanisms in this model are the mean structure effect ΔS_i, the mean environmental effect ΔE_i, and the mean effect of interaction between environment and competition ΔI_i, known as the storage effect. Stabilizing effect (or destabilizing effect if negative) of each mechanism is a community-average measure as each mechanism averaging over all species as invader ($\overline{\Delta S}$, $\overline{\Delta E}$ and $\overline{\Delta I}$). Fitness inequality effect is measured as any deviation of the individual level mechanisms from their stabilizing effect: $\Delta S_i - \overline{\Delta S}$, $\Delta E_i - \overline{\Delta E}$ and $\Delta I_i - \overline{\Delta I}$ each labeled as δS_i, δE_i and δI_i

The quantity ΔS_i measures shifts in mean structure between invader and resident states that occur in a variable environment (Appendix II). Our previous study shows this mechanism is strong only when there is a large shift in size structure between sizes that vary greatly in their contribution to population growth (Yuan and Chesson, in progress). Variation in reproduction leads to a low-density advantage in reproduction and more seedling recruitment drives size structure towards more smaller individuals in invader state compared with the resident state. Variation in

individual growth leads to low-density advantage in growth, and larger individual growth drives size structure towards more larger individuals in invader state. Shift in structure only promotes coexistence when size structure shift in direction with demographic advantages. It undermines coexistence otherwise. Thus, this mechanism highly depends on both the shapes of demographic schedules and environmental variation. The shapes of demographic schedules determine the relative contributions of individuals of different sizes to population growth. Environmental variation determines the direction of the shift in structure.

The quantity ΔE_i measures differences in mean environmental effect between invader and resident. The approximation for mean environmental effect comes down to a ln ratio of environmental variation (on exponential scale) in each process weighted by relative importance of each process, the p's (Yuan and Chesson, in progress):

$$\Delta E_i \approx \ln\left(\frac{p_{ibg}e^{\left(\sigma_{ib}^2 + \sigma_{ig}^2\right)/2} + p_{ig}e^{\sigma_{ig}^2/2} + p_{ib}e^{\sigma_{ib}^2/2} + p_{is}}{p_{rbg}e^{\left(\sigma_{rb}^2 + \sigma_{rg}^2\right)/2} + p_{rg}e^{\sigma_{rg}^2/2} + p_{rb}e^{\sigma_{rb}^2/2} + p_{rs}} \right). \qquad (7)$$

The p's are average fractional contribution to population growth from recruitment (p_b), initial growth of offspring (p_{bg}), growth of established individual (p_g), survival (p_s). They add up to one. Each fraction is measured in either invader or resident state indicated by their subscripts.

Approximation in Eq. (7) indicates that large magnitude of ΔE_i is due to two reasons: strong asymmetries in σ^2, sensitivity in environmental responses; strong asymmetries between species in p's, relative importance in the contribution of the processes to population growth rate. In particular, the magnitude ΔE_i is large when one species has strong sensitivity to environment in processes important to its population growth, and the

other species does not. However, asymmetries in sensitivity to environment, which are density-independent, lead to fitness inequality only. The relative fractional contribution as measured by the p's, however, can change as the mean structure shifts with species' density. Thus we predict that a strong stabilizing or destabilizing effect of ΔE_i incurred by such a density dependent loop can only be seen with a significant effect of the shift in size structure. Based on the approximation, our hypothesis is that ΔE_i contributes to stabilizing coexistence only when the size structure in the invader state results in a greater p compared with resident state for the process sensitive to the environment. But such a condition is restrictive.

Among all mechanisms, the condition for a stabilizing effect of the storage effect ΔI_i can be met most easily and the storage effect is usually the major contributor to the stability of coexistence (Chesson 2003, 2008). The storage effect measures differences in ability to decouple environment with competition between invader and resident. For it to promote coexistence, two critical requirements must be satisfied (Table 1). First, covariance between environment and competition (covEC), which is measured by a formal statistical covariance over time between environment and competition, must be higher in the resident state than in the invader state (Chesson 2008). Such differences in covariance arise easily unless the invader species has the exact same pattern of variation in its environmental response as the resident. A resident species in a favorable environment imposes strong self-limitation through intraspecific competition—a high value of covEC. The invader has opportunities to escape competition when the resident species is suffering from the environment—a low value of covEC. The second critical component of the storage effect is buffered

population growth. The buffer is due to the subadditive (negative) interaction between environment and competition in population growth. As a result, increasing competition does not have such a strong limitation on population growth for a species in unfavorable environment as on species in favorable environment. Buffered population growth arises easily in nature, e.g. from the long life span of long-lived organisms and dormant stages of short-lived organisms. We defined storage (ψ) as a measure for this buffer. It is the absolute value of the negative interaction between environment and competition divided by sensitivity competition, i.e. it is measured on the natural scale.

Life history processes sensitive to both environment and competition can all lead to the storage effect. In our model the storage effect can arise from both reproduction ΔI_b and individual growth ΔI_g. The approximation for the storage effect shows the key effects of a complex life-history on coexistence because the storage effect can be summarized by the p's, the fractional contributions to population growth through key processes (Table 1). As a process increases on average in its contribution to population growth, the corresponding buffer and covEC both increase (Yuan and Chesson in progress, Table 1). In the simple situation where species are independent in their responses to the environment, the storage effect an invader experiences depends only on the life history of the resident species (Table 1, Appendix II). From the approximation, we predict that a process leads to substantially storage effect when the average importance to population growth and the sensitivity to environment of a process are aligned. With contrasting life history between species, it is reasonable to expect strong asymmetries in storage effects experienced by different species.

Table 1 Functional components of the storage effects

ΔI	Formula	Functional component		
		Storage	θ	covEC χ
ΔI_{ib}	$\psi_{\mathrm{rb}}\chi_{rb}$	$\psi_{\mathrm{rb}}=\dfrac{\left(p_{\mathrm{rb}}+p_{\mathrm{rbg}}\right)p_{\mathrm{rs}}}{1-p_{\mathrm{rs}}}$	$\theta_{\mathrm{rb}}=\dfrac{p_{\mathrm{rb}}+p_{\mathrm{rbg}}}{1-p_{\mathrm{rs}}}$	$\chi_{\mathrm{rb}}=\theta_{rb}\sigma_{\mathrm{rbb}}+\theta_{\mathrm{rg}}\sigma_{\mathrm{rbg}}$
ΔI_{ig}	$\psi_{rg}\chi_{rg}$	$\psi_{\mathrm{rg}}=\dfrac{\left(p_{\mathrm{rg}}+p_{\mathrm{rbg}}\right)p_{\mathrm{rs}}}{1-p_{\mathrm{rs}}}$	$\theta_{\mathrm{rg}}=\dfrac{p_{\mathrm{rg}}+p_{\mathrm{rbg}}}{1-p_{\mathrm{rs}}}$	$\chi_{\mathrm{rg}}=\theta_{\mathrm{rg}}\sigma_{\mathrm{rgg}}+\theta_{rb}\sigma_{\mathrm{rbg}}$
ΔI_i		$\psi_{\mathrm{rb}}\chi_{\mathrm{rb}}+\psi_{\mathrm{rg}}\chi_{\mathrm{rg}}=\left[\begin{array}{l}\left(p_{\mathrm{rbg}}+\overline{p}_{\mathrm{rb,g}}\right)\left(\chi_{\mathrm{rb}}+\chi_{\mathrm{rg}}\right)\\ +\left(p_{\mathrm{rb}}-\overline{p}_{\mathrm{rb,g}}\right)\chi_{\mathrm{rb}}+\left(p_{\mathrm{rg}}-\overline{p}_{\mathrm{rb,g}}\right)\chi_{\mathrm{rg}}\end{array}\right]p_{\mathrm{rs}}$		

Table adapted from Table 3 in (Yuan and Chesson, in progress) Legends: ψ_{b} storage due to reproduction; ψ_{g} storage due to individual growth; $\chi_{\mathrm{b}}=\mathrm{cov}(E_{\mathrm{b}},C)$; $\chi_{\mathrm{g}}=\mathrm{cov}(E_{\mathrm{g}},C)$; $\sigma_{\mathrm{bg}}=\mathrm{cov}(E_{\mathrm{b}},Eg)$; $\sigma_{\mathrm{bb}}=\mathrm{Var}(E_{\mathrm{b}})$; $\sigma_{\mathrm{gg}}=\mathrm{Var}(E_{\mathrm{g}})$;

Missing from from Eq (6) is the mean effect of competition ΔC_i. This mean effect

of competition can be partitioned into a linear term and the relative nonlinearity ΔN_i.

It is omitted because when two species have identical mortality schedules, the

differences in the effect of competition between invader and resident are limited.

Cases considered

We mainly study two species with contrasting fecundity and growth schedules

both in mean and shape. One species has an advantage in mean fecundity: it starts to

reproduce right after seedling establishes and has mean reproduction increase more

rapidly with size (Fig. 1). The other species has an advantage in mean individual

growth with competitiveness for growth increasing rapidly with size, but its

reproduction is delayed and increases slowly with size. For a comparison, we also

consider an extreme case where we keep the mean of the schedules unchanged but

change their shapes to be flat, i.e. size independent. The fecundity and growth function of

species are chosen so that the species have equal mean fitness in a constant environment

(Appendix III).

To generalize our findings, we are able to vary the differences in demographic

schedules between species along a continuous gradient in a tradeoff from the strongly

asymmetric case (Fig. 1 black) to a symmetric case where the species are at the same

point on the tradeoff (Fig. 1 grey). Along the gradient, demographic schedules are the

weighted averages of two extreme schedules. Changing the weights morphs one into the

other (Appendix III). Weights are obtained from analytical solutions so that along the

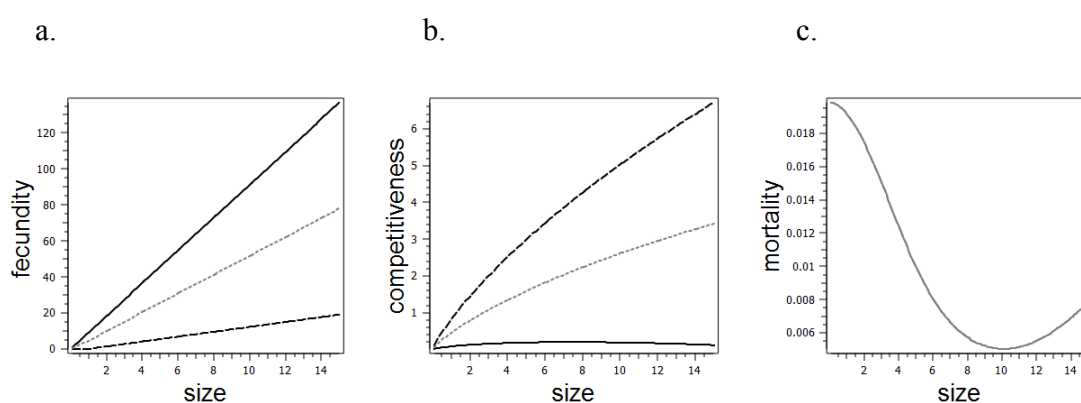gradient species have equal fitness in a constant environment (Appendix III).

Fig. 1. Equilibrium demographic functions for species with fecundity growth trade-off, comparison between strongly asymmetric (black) end and symmetric (grey) end of the tradeoff. When asymmetric, species 1 has a mean advantage in reproduction (solid, a) and a mean disadvantage in growth (solid, b); species 2 has a mean disadvantage in reproduction (dashed, a) and a mean advantage in growth (dashed, b). Both species have identical mortality schedule with size (c).

Results

Constant environment

In this model because all species are limited by the space in the same way, no stabilizing effect exists in a constant environment (Fig. 2). There is a unique solution for the difference in mean environmental responses in reproduction between species that allow species to have neutral coexistence (Fig2 a, Appendix III). Either side of this value, one of the species excludes the other, i.e. any deviation in mean fitness differences leads to exclusion of one species. In a constant environment, a tradeoff in life history processes can only reduce the average fitness differences between species. Though such equalizing effects do not allow stable coexistence alone, they reduce the magnitude of the stabilizing effect required for stable coexistence (Chesson 2000).
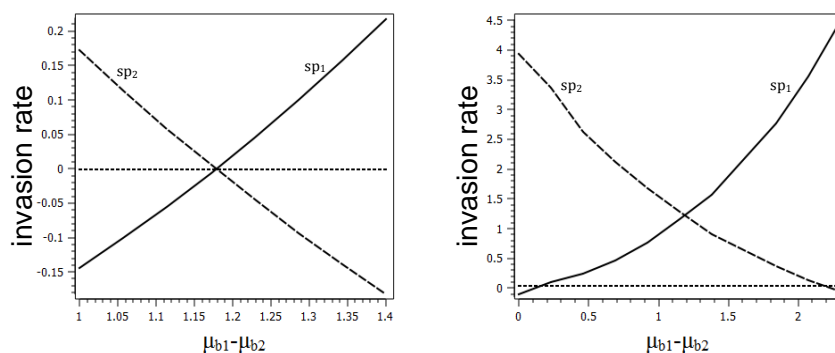

Figure 2. Coexistence region measured by range of differences in mean environment responses in reproduction (μ_b) between species that allows successful invasion of both species. Comparisons are made between constant environment where the region is zero (a) and variable environment where there is a nonzero region (b). Details of parameterizations in Appendix III.

A fitness advantage in life-time reproduction from one species can be equalized by its competitor having an advantage in individual growth (Fig. 3). However there is an exception: a fecundity-growth tradeoff cannot equalize fitness in the extreme cases where fecundity and mortality are insensitive to size (Fig. 3, dashed line). The reason for this is that, regardless of the size dependence, ultimately birth rates and death rates determine the fitness. If size does not affect any of these processes, growth in size is

irrelevant. Thus, individual growth, regardless of how it changes with size or differs between species, cannot compensate for fitness differences caused by fecundity or survival schedules. While this extreme case might be very unlikely in nature, we use it as a reference point for our study.
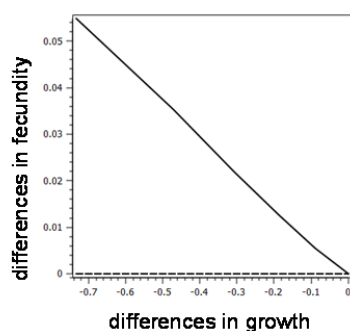

Figure 3. Tradeoffs in life-time growth rate and life-time reproduction for two species that allow neutral coexistence in constant environment (solid). In extreme cases, with flat mortality and fecundity schedules (dashed), species have to be identical in fecundity for neutral coexistence, regardless of differences in life-time growth. Details of parameterizations in Appendix III.

Variable Environment

Stable coexistence, in our model, arises only when there are species-specific responses of life-history traits to environmental variations (Fig. 2 b). However, differences in life-history schedules are critical in determining the relative importances of different fluctuation-dependent mechanisms. Previous work with the unstructured lottery model (Yuan and Chesson In review) showed that the magnitude of fluctuation-dependent mechanisms increases proportionally to the sensitivity, σ^2_b, of the species' fecundity to environmental variation. This finding is generalized to a linear function of σ^2_b and σ^2_g in the structured case (Yuan and Chesson, in progress), and in the analytical approximation to the storage effect (Table 1). Thus, there appears to be no need to study

these mechanisms for a range of σ^2_b and σ^2_g. For simplicity, in this study, we fixed

these sensitivities (σ^2_b for reproduction and σ^2_g for growth) at either 0 or 1.

The storage effect

With contrasting life history schedules (Fig. 1), two species experience storage

effects of very different magnitudes (Fg. 4, 5, 6). The more contrast there is in life-

history schedules, the stronger the asymmetries in storage effects experienced by the

different species (Fig 5, Fig. 6). The primary aspects of the difference in life history

schedules that matters for the storage effect are the population level demographic

properties. With environmental responses being independent between species, the

storage effect experienced by an invader is created by the resident species. A resident

can lead to a strong storage effect when its life history processes that on average

contribute strongly to population growth are also strongly sensitive to the

environment (Table 1). Tradeoffs between species in life histories drive the

asymmetries in the storage effect through altering the average fractional contribution

of each process to population growth (p_r in Table 1.). The species with an advantage

in fecundity have a larger fractional contribution of reproduction (p_{rb}) than the

fractional contribution of individual growth (p_{rg}); the species with an advantage in

individual growth has p_{rg} larger than p_{rb}. The functional components of the storage

effect (buffers and covECs) can both be expressed by the p_r values. The storage effect

for a given population growth component (reproduction or individual growth) is an

increasing function of the p_r value for that component, and also the p_r value for

seedling growth (Table 1). Thus, the relative importance of the two sorts of storage

effect, assuming that reproduction and individual growth are equally sensitive to the

environment, depend on the relative values of p_{rb} and p_{rg}. For a species with an average

advantage in reproduction, variation in reproduction can lead to a stronger storage effect

for its competitor than does variation in growth (Fig. 5, black). Reciprocally, for the

species with an advantage in individual growth, variation in growth can lead to a stronger

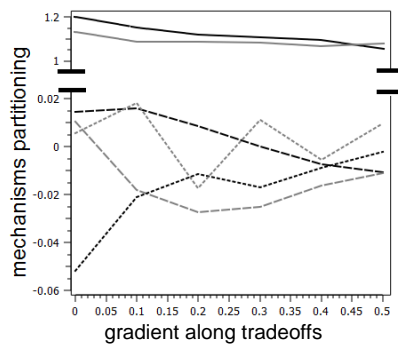storage effect for its competitor than does variation in reproduction (Fig. 5, grey).

Figure 4. Change of individual level mechanisms between two species along the continuous gradient of a fecundity-growth tradeoff from strongly asymmetric (x = 0) to symmetric (x = 0.5). Storage effect: solid lines, and other mechanisms below the scale break. Species with advantage in reproduction in black, and species with advantage in growth in grey. Details of parameterizations in Appendix III.
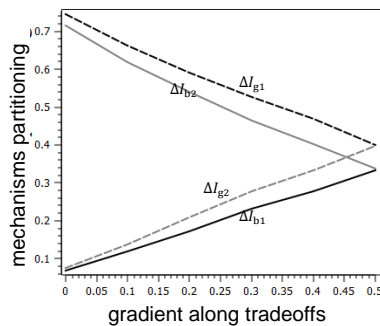
Figure 5. Change of individual level storage effects (in approximation) between two species along the continuous gradient of fecundity growth tradeoff from strongly asymmetric (x = 0) to symmetric (x = 0.5). Storage effect in reproduction is solid and storage effect in growth is dashed. Species with advantage in reproduction(sp1) in black, and species with advantage in growth (sp2) in grey. Details of parameterizations in Appendix III.

When both species have reproduction and individual growth sensitive to environment,

neither species will be advantaged in both storage effects (Fig 5). The storage effect in

growth can compensate for changes in the storage effect in reproduction. But if there is a

strong contrast in the relative importance of the process sensitive to environment, e.g.

both species only vary in reproduction or only vary in growth, strong asymmetries in storage effects lead to a strong fitness inequality between the two species (Fig. 6 a, c). These differences are reduced as the life-history schedules of the species become more similar.

So far we have only investigated cases when two species have independent environmental responses. In Appendix II, the quadratic approximation is generalized to the case where the species are correlated. Then the storage effect experienced by a species depends also on its own p's, i.e. the fractional contributions to population growth of the species itself, the p_i's. However, these contributions will not be high unless the species have strongly correlated environmental responses.

When species are strongly opposite in their responses to the environment (a strong negative correlation between species), increasing contribution to population growth of the process most sensitive to environment increases the storage effect a species itself experiences as invader (Appendix II). On the other hand, when species are highly positive-correlated, increasing importance of the process most sensitive to environment decreases the storage effect that the species itself experiences as invader (Appendix II). Invader p_i's further depend on invader structure that shifts with fluctuations, though the effects can be very limited as in the section below on

The storage effect is the strongest contributor to stabilizing coexistence among the three mechanisms (Fig 5, 6b, 6d). The stabilizing effect is strong when the storage effect experienced by each species is strong. Life-history traits affect the storage effect through the values of the p_r's as discussed above, but given these values, the shapes of the life-history schedules have no additional effect on the storage effect

according to the quadratic approximation to its magnitude (Table 1). This prediction of the quadratic approximation is supported by simulation comparing flat fecundity and mortality schedules with others (Fig. 1), where the storage effect changes very little when the p_r's do not change (Fig. 7). However, the overall mechanism magnitude (invasion rate) is dramatically different due to (ΔS) and mean effect of environment (ΔE) becoming important in this case, as discussed next.

Environmental variation and the mean structure

Besides the storage effect, differences in life histories affect the mean environment effect ΔE and the mean structure effect ΔS. Between the two, ΔE is found to be much stronger. The structure can change between resident and invader states in a fluctuating environment because the invader growth rate becomes nonzero. The mechanism ΔE measures invader-resident differences in population level responses to mean environment effect at a fixed level of competition. It is sensitive to population structure. Fig. 6 shows that it has only a weak stabilizing or destabilizing effect, but much stronger effects on fitness inequalities arising from differences in life histories between species.

Consistent with our prediction from the approximation Eq. 7 in the theory section above, strong fitness inequalities arise from ΔE if the two species differ strongly in the relative importance of processes sensitive to the environment (Fig. 6). When one species has a process with mean advantage being sensitive to the environment and its competitor does not, the species receives a mean fitness advantage from ΔE, and its competitor gets a mean fitness disadvantage from ΔE. For example, when both species have only reproduction sensitive to the environment, one with a mean advantage in reproduction

benefits from ΔE and the other one with a mean disadvantage in reproduction suffers from a negative ΔE (Fig. 6a). The reverse applies when both species have only individual growth sensitive to the environment (Fig. 6b). This inequality not only increases with the contrast in the relative importance of reproduction and individual growth to population growth (Fig. 6), but also differences between species in their sensitivities to the environment, which can be inferred from Eq. 7. Interestingly, fitness inequality due to the mean effect of environment varies exactly in the opposite way to inequality in the storage effect (Fig. 6). Thus, fitness inequalities of the two mechanisms get equalized (Fig. 6).

A community average effect of the mean environment effect $\overline{\Delta E}$ only arises with changes in the fractional contributions of critical processes to population growth between invader and resident states, in forms of differences between the p_i's and p_r's. These changes in p's occur because of shifts in the size structure, and individuals of different sizes contribute differently to population growth. In fact, $\overline{\Delta E}$ can be stabilizing as well as destabilizing. It depends on how the mean structure shifts as well as the shapes of the demographic schedules that determine how demographic traits change with size. In general, the magnitude of $\overline{\Delta E}$ is very small. For species with life history schedules in Fig. 1, the community average $\overline{\Delta E}$ is minimal compared with the stabilizing effect of the storage effect (Fig. 6). Consistent with our predictions in the theory section from Eq. 7, the limited effect of $\overline{\Delta E}$ is due to the limited effect of shifted in structure (Fig. 6).

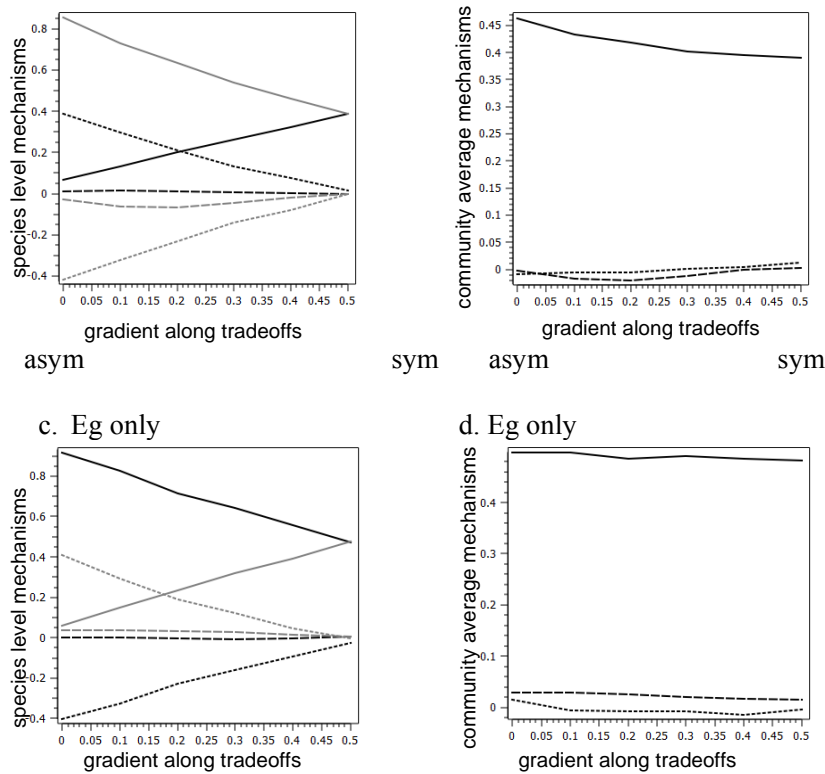a. Eb only   b. Eb only

Figure 6. Changes of coexistence mechanisms along the gradient of fecundity-growth tradeoff from strongly asymmetric (x = 0) to symmetric (x = 0.5). Panels (a) and (b) plot the individual level and community average mechanisms respectively for coexistence of species with only reproduction sensitive to environment. Panels (c) and (d) plot the individual level and community average mechanisms respectively for coexistence of species with only growth sensitive to environment. The mechanisms plotted are storage effect (solid), shifted in structure ΔS (dashed), ΔE (dotted). For plots with individual mechanisms (a and c), species with advantage in reproduction (Sp1) in black, and species with advantage in growth (sp2) in grey. Details of parameterizations are in Appendix III.

The effect of shifted mean structure, ΔS, strongly depends on the shapes of the demographic schedules. We see shifts in structure having important community average effects under extreme situations with flat fecundity and mortality schedules (Fig 7). When both species have growth varying, size structure will shift dramatically increasing the fraction of larger individuals from the resident to the invader state. In this case both $\overline{\Delta S}$ and $\overline{\Delta E}$ are destabilizing (Fig. 7). The total destabilizing effect due to shift in structure is close to the magnitude of the stabilizing effect of the storage effect, acting

strongly to cancel out coexistence promoting effect of storage effect in growth. The effect of shift in structure ΔS are destabilizing because larger individuals does not have demographic advantage. The population density is smaller with more larger individuals, reducing the overall contribution to population growth. The mean effect of environment $\overline{\Delta E}$ further enhances the destabilizing effect under shifted structure. As there are fewer individuals contributing to recruitment and individual growth, there is a reduction in the overall fractional contribution from processes sensitive to environment. Structure shift towards having more smaller individuals under variation in reproduction will do the opposite: there will be a significant stabilizing effect of $\overline{\Delta S}$, enhanced by a stabilizing effect of $\overline{\Delta E}$ (Fig. 7).
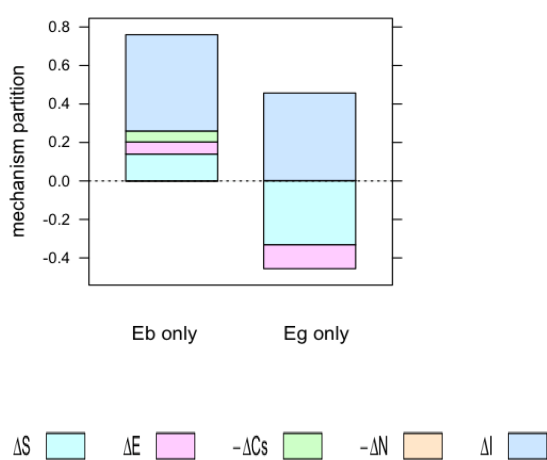

Fig. 7 partitioning of community average mechanisms in extreme cases with flat fecundity and mortality schedule, comparison are made between Eb only and Eg only cases. The life time reproduction and mortality, as well as the competitive schedule are kept the same with those in other examples illustrated. Details of parameterization are in Appendix III.

Discussion

Stable coexistence generally requires differences between species in the ways they use the environment. Species differ in many ways, but which of these differences contribute to stable species coexistence? Differences in life-history traits are easily observed and measured (Westoby et al. 2002), and life-history tradeoffs have been widely discussed as a potential coexistence mechanism (Nakashizuka 2001, Kneitel and Chase 2004). However, many studies question the significances of tradeoffs as in general it is not clear that they lead to different uses of the environment by different species (Condit et al. 2006, Esther et al. 2011). A response is that even though life-history differences may not directly lead to different uses of the environment, they may interact with other mechanisms based on such differences, and as a consequence alter the possibilities for species coexistence. Understanding such effects is best done by quantifying species coexistence mechanisms allowing interactions between processes to be partitioned out and assessed.

Using a continuous-size structured lottery model, we show how it is possible to quantify coexistence mechanisms for communities with complex life histories. The goal is to understand the role of complex life histories in species coexistence. We consider both constant and variable environments. In a constant environment, we find that life-history tradeoffs alone do not lead to stable coexistence. This is consistent with the fact that there is only a single limiting density dependence factor in our model, which is the space available for seedling recruitment and tree growth. Life-history tradeoffs between species in this context only affect average fitness differences between species. They thus affect the identity of the dominant species and how rapidly it excludes the other species.

A perfect tradeoff would equalize the mean fitness between species and lead to neutral coexistence.

In a variable environment life-history tradeoffs continue to affect mean fitness differences, but they can also affect the strength of stable coexistence mechanisms that arise in a variable environment. Our model assumes that three different processes may be sensitive to environmental variation, namely, recruitment, individual growth during recruitment and during post-recruitment phases. We assume that the latter two are perfectly correlated within a species. Processes sensitive to environmental fluctuations generate coexistence mechanisms. Nonetheless, the relative importances of the different coexistence mechanisms are affected by the mean relative contributions to population growth of these processes and how they change with size. Tradeoffs in life history alter the magnitude of the mechanisms and their asymmetry between species by changing these mean contributions.

Variation in reproduction and individual growth can each independently lead to three mechanisms. A mean structure effect measures the direct effect of shift in mean structure on population growth rate. A mean environment effect measures the population level average response to environment. The storage effect measures the ability to decouple environment from competition. The storage effect, as the most significant mechanism, acts asymmetrically between species because of tradeoffs in mean population level properties between species. Between two species with a fecundity-growth tradeoff, a species benefiting from a strong storage effect due to reproduction will likely not benefit much from a strong storage effect due to growth, and vice versa. The mean structure effect depends on differences in the contributions

to population growth from cohorts of different sizes. The asymmetries between species of the mean structure effect will be large if the species have opposite patterns of size dependence of vital rates. The asymmetry in the mean environment effect depends on both differences in population level properties and differences in the size-dependence of a process. Species obtain a mean fitness advantage from a mean environmental effect if the important processes for population growth in that species are more sensitive to environmental fluctuations than they are in the other species. A low density advantage arises if shift in size structure enhances the mean importance of processes sensitive to environmental fluctuations. Nevertheless, as will be discussed later, shifts in structure have only weak effects except under very restrictive conditions.

Despite asymmetries between species introduced by tradeoffs in life histories, it is by far easiest to see strong stabilizing effects from the storage effect, and they are in general positive for both species. The storage effect promotes species coexistence when a species exert stronger self-limitation by more active resource consumption in a favorable environment. Self-limitation arises most strongly from the process most demanding for resources on average, which in turn is the process most important on average for population growth. Environmental sensitivity of this process leads to strong covariance between the environmental response and competition when a species is in the resident state, which benefits the invader. The more important a process is for population growth, the greater the effect of its sensitivity to the environment in creating the storage effect. Therefore, we will expect strong stability of coexistence to be contributed by the storage effect when the sensitivity of a life-history process to variation in the environment is aligned positively with the tradeoff between life-history processes. Thus, for a strong

storage effect, a species with high environmental sensitivity in fecundity should have an average advantage in fecundity relative to a species with high sensitivity in individual growth, which should have an advantage in individual growth.

In contrast to the storage effect, the mean environmental effect (ΔE) and mean structure effect usually have opposite signs for species with contrasting life histories and contrasting relative amounts of variation in growth and variation in reproduction. As a consequence, the fitness inequality resulting from the mean environmental effect to a large degree compensates for the asymmetry of the storage effect. The opposite species differences resulting from the storage effect and the mean environment effect tend to equalize the overall ability of each species to recover from a low density. Nevertheless, the mean environmental effects often get averaged out at community level and do not contribute much to the stability of coexistence. This is especially true when both reproduction and growth vary where their mean effects of variation cancel.

Important effects of mean structure shifts on coexistence (ΔS) occur in very restricted circumstances. The shift must have net consequences for growth of the total population. This means that a shift must have a major effect on the number of individuals in size ranges with much stronger than average contributions to population growth. This condition, requires specific combinations of variation in response to the environment and shapes of demographic schedules. The most realistic schedules, such as those in Fig. 1 , do not lead to substantial shifts in structure, and have no substantial effect on long-term growth of either species. Two extreme examples of demographic schedules where a shift in structure can have significant effects are a flat fecundity schedules (Fig. 7) and a delayed fecundity schedule

(unpublished work). Under a flat fecundity schedule, cohorts of smaller individuals contribute substantially more to population growth than cohort of larger individuals. The opposite occurs under the delayed fecundity schedule. For a significantly positive effect of size structure, species with a flat fecundity schedule must be associated with strong variation in reproduction so that size structure shifts towards more smaller individuals. Species with a delayed fecundity schedule must have strong variation in growth that drives size structure towards more larger individuals. These conditions maybe difficult to achieve in nature. Moreover, they get weakened when reproduction and growth both vary.

When strong effects of mean structure occur, they not only affect ΔS, the direct measurement of the role of mean structure, but the underlying shift in structure also affects ΔE. By increasing the average contribution to population growth of processes that are sensitive to environment when a species is in the invader state, a stabilizing effect of the mean environment can result. However, given the rarity of strong effects of mean structure, these results may be of more academic interest than applicable in nature.

Our study intends to relate biology to general understanding of the mechanisms. We show that life-history tradeoffs, rather than being a mechanism for species coexistence alone, instead affect coexistence through interactions with other factors, specifically environmental variation, and other mechanisms such as the storage effect. Merely evaluating life-history tradeoffs without consideration of other factors is insufficient to understand their effects on stabilizing coexistence. Our model developments synthesize life history processes over the life cycle and quantify their interactions with other processes to determine their overall effects on mean fitness differences and stabilizing

mechanisms. Only a few critical quantities are needed to summarize the effects of a complex life history to determine the relative importance of different coexistence mechanisms.

A key finding of our study is that species differences in sensitivity to environmental variation have a major effect on the magnitudes of the contributions of life-history tradeoffs to species coexistence. The most important positive effects on coexistence occur when the process contributing most strongly to population growth for a species are the processes most sensitive to environment variation. In nature, there is strong evidence for differences in sensitivity to environmental variation (Wright et al. 2005, Vincent et al. 2009). There is evidence in forest trees for more competitive species being more sensitive to environment associated with a growth rate - herbivory tradeoff (Kelly and Bowler 2002, Kelly and Hanley 2005). Fast growing trees tend to be more responsive than slow growing trees to favorable environment to growth, but slow growing trees are more tolerant of resource shortage (Baker et al. 2003, Ouedraogo et al. 2013). Highly sensitive reproduction very possibly carries a mean advantage as well. In the example of masting, species are highly sensitive to the environment and it is suggested that mass production of seeds is not only taking advantage of a favorable environment but also is possibly a predator-satiation strategy, or pollinator-attraction strategy (Kelly and Sork 2002). Coexisting animal species may also show contrasting sensitivities in behavioral responses to the environment. Our study has clearly laid out how these sensitivity differences lead to stabilizing niche differences.

Though our results are illustrated for a simple case of species with a fecundity-growth tradeoff, the methodology applies in general. The major effect of a complex life-history on stable coexistence depends on whether processes most important to population growth are on average most sensitive to environment. If a tradeoff involves large differences in mortality, such as growth-mortality tradeoff (e.g forest trees), relative nonlinearity may be significant when species with high death rates are associated with much larger sensitivity differences (Yuan and Chesson In review). Under these conditions, higher sensitivity to environment in species with high individual growth rates and high death favors the competitor when it is at low density through the mechanisms termed relative nonlinearity (Yuan and Chesson, in review). A high sensitivity in growth rates of this species also compensate for the weakening buffer in the storage effect due to the high death rate.

The assumption of lottery competition for space means that our model best applies to organisms where the resources required for recruitment are sequestered by the living organisms, and released on death. Examples include sessile organism such as plants, intertidal marine invertebrates, coral, as well as animals such as coral reef fishes. The form of competition can be easily modified for more accurate descriptions of other communities, but our fundamental conclusion will not be affected. A better acknowledgement of not only which mechanisms are present, but also how their relative importances are affected, are the key to studying species coexistence in various systems. Our study offers a guide to understand the role life histories play.

Appendix I

Model will be illustrated using forest trees. Critical variables in the model are the total available space, $S(t)$, from deaths during the interval t to $t + 1$, and the total demand, or requirement, for space, $R(t)$ (Details in Table A.1). As explained above, this demand for space is the total new space needed to achieve the largest potential of reproduction and growth under unlimited space supply. Since the space available is not unlimited, competition occurs. The magnitude of competition is evaluated as the ratio of demand to supply, which is given on the log scale as

$$C(t) = \ln R(t)/S(t), \tag{A.1}$$

and referred to as the competitive response. Individuals of all species and sizes compete in same resource pool, and competition reduces their actual establishment and growth. Competition for space comes from two processes: recruitment to the seedling cohort and subsequent growth of individuals in the established cohorts.

Trees in cohort c of species j has size a_{jc} and density N_{jc}, both change with time but t is omitted for notational simplicity. Resource supply S from Eq A.1 is summed over death occurred over all cohorts of all species, based on a species-specific size-dependent mortality function $m_{a_{jc}}$:

$$S = \sum_{c,j} N_{jc} a_{jc} m_{a_{jc}}. \tag{A.2}$$

But in this study we assume species have identical mortality function $m_{a_{jc}}$.

Demand for space from seedling depends on two factors: the fecundity schedule $k_{j,a_{jc}}$ determines the size-dependency in fecundity, which is time invariant and further weighted by the competitiveness in seedling establishment c_{sj}; the other factor $e^{E_{b_j}(t)}$

captures fluctuation in reproduction due to environmental variation, where the quantity E_{bj} is defined as the environmental response in reproduction.

The above description gives the following equation for the species-specific fecundity function for per capita seed production from individuals from cohort c of species j:

$$k_j(a_{jc}, t) = c_{sj} k_{j,a_{jc}} e^{E_{bj}(t)}.$$ A.3

Total number of seedling produced by species j N_{sj} is summed over seedling produced by each cohort:

$$N_{sj}(t+1) = \sum_c c_{sj} k_{j,a_{jc}} e^{E_{bj}(t)} N_{jc}$$ A.4

The total demand for space from seedling recruitment is Eq. A.4 summed over species. Demand for space also comes from individual growth from both the germinated seedling cohort and established cohort that escaped death. The potential growth without resource limitation for cohort c of species j is determined by two components. A size-dependent growth schedule $c_{j,a_{jc}}$, also called the competitiveness schedule, determines how ability to grow change with size. We specify the competitiveness of seedling growth as c_{sj}. The temporal fluctuation in the growth potential depends on $e^{E_{gj}(t)}$, where E_{gj} is defined as the environmental response in growth. The above description gives the species-specific growth function $c_j(a_{jc}, t)$, which describes the per capita demand for space to growth from individual in cohort c of species j as:

$$c_j(a_{jc}, t) = c_{a_{jc}} e^{E_{gj}(t)}$$ A.5

Total demands for space, R from Eq.A.1, is the sum over space required for seedling establishment, seedling growth, and growth of established saplings and adults:

$$R = \sum_j \sum_c \left(\left(a_{sj} + c_{sj} e^{E_{gj}} \right) c_{sj} k_{j,a_{jc}} e^{E_{bj}} + c_{j,a_{jc}} e^{E_{gj}} \left(1 - m_{a_{jc}}\right) \right) N_{jc} \qquad \text{A.6}$$

The actual number of seedling established as a new cohort of species j N_{nj} is subject to competition:

$$N_{nj}(t+1) = \sum_c c_{sj} k_{a_{jc}} e^{E_{bj}(t)-C(t)} N_{jc} \quad . \qquad \text{A.7}$$

We assume seedling growth after germination is not subject to competition as competition already occur during their establishment. The size of the established seedling is therefore:

$$a_{nj}(t+1) = a_{sj} + c_{sj} e^{E_{gj}(t)} \qquad \text{A.8}$$

where a_{sj} is a species-specific constant for initial seedling size. Thus the total area allocated to seedling recruitment of species j is

$$A_{bj} = a_{nj} N_{nj} \ . \qquad \text{A.9}$$

The growth of individuals in the established cohorts is reduced by competition

$$a_{jc}(t+1) = a_{jc}(t) + c_{a_{jc}(t)} e^{E_{gj}(t)-C(t)} \qquad \text{A.10}$$

The total space occupied by the established cohorts of species j in the t+1 is

$$A_{gj} = \sum_c a_{jc}(t+1)\left(1 - m_{a_{jc}}\right) N_{jc}(t) \qquad \text{A.11}$$

where $m_{a_{jc}}$ is the mortality rate for individuals in cohort c of species j. The population

growth rate of species j is evaluated as change in log area occupied by the whole

population from one time to another as:

$$r_j(t+1) = \ln A_j(t+1) - \ln A_j(t) \qquad \text{A.12}$$

where $A_j = A_{bj} + A_{gj}$.

Table A.1. General notation

Symbol	Definition
capital C	Competitive responses
$R; S$	Total demand and supply for space
subscript c	Index for cohort
subscript j	Index for species, in particular i for invader, r for resident
$a_{jc}; a_{nj}$	Size of individuals in cohort c and seedling cohort (n) of species j
$k_{j,a_{jc}}; c_{j,a_{jc}}; m_{a_{jc}}$	fecundity schedule, growth (competitive) and mortality schedule
E_{bj}, E_{gj}	Environmental response in reproduction and in growth respectively
$k_j(a_{jc}, t)$	Fecundity per individual in cohort c of species j
c_{sj}	Competitiveness in seedling establishment
$N_{sj}; N_{nj}; N_{jc}$	Density of seedling germinated, seedling established respectively and cohort c
$A_j; A_{bj}; A_{gj}$	Total Area, area of the new seedling cohort, and area of established cohorts
$r_j(t); \bar{r}_i$	The population growth rate; long-term low density growth rate of invader
β_j	The scaling factor, sensitivity of growth rate r_j to competition.
ξ_i	Average fitness differences between invader and resident
$\bar{A}$	The overall stabilizing effect
$\Delta S_i, \overline{\Delta S}$	Mean effect of size structure, and its community average effect
$\Delta E_i, \overline{\Delta E}$	Mean environmental effect and its community average effect
$\Delta I_i, \Delta I_{ib}, \Delta I_{ig}, \overline{\Delta I}, \overline{\Delta I_b}, \overline{\Delta I_g}$	The overall storage effect; storage effect in reproduction; storage effect in growth and their corresponding community average effect
$\chi_{bj}; \chi_{gj}$	Cov(E_{jb}, C) and Cov(E_{jb}, C) for invader ($j = i$) and resident ($j = r$)
$\psi_{bj}; \psi_{gj}$	storage for buffer in reproduction and buffer in growth ($j = i$ or r)

$\theta_{bj}; \theta_{gj}$	Sensitivity of C to E_b; Sensitivity of C to E_g ($j = i$ or r)
$p_{sj}, p_{bj}, p_{bgj}, p_{gj}$	Proportional contribution of survival, reproduction, seedling growth, sapling growth to population growth ($j = i$ or r)

Appendix II

Exact form of mechanisms partitioning

The population growth rate in Eq.2 can be expressed as a function of environment E, competition C and structure S.

$$r_j = g(\mathbf{E}_j, C, S_j) = \ln G_j(\mathbf{E}_j, C, S_j) \qquad \text{A.13}$$

Rearrangement of growth rate partition it to several components:

$$\begin{aligned}
r_j &= g_j(\mathbf{E}_j, C^{\{i\}}, S_j^{\{i\}}) \\
&= g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{*\{i\}}) \dots\dots\dots\dots\dots\dots\dots\dots\dots\bar{r}_j^{'} \\
&+ g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{\{i\}}) - g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{*\{i\}}) \dots\dots\dots\mathscr{S}_j^{\{i\}} \\
&+ g_j(\mathbf{E}_j, C^{*\{i\}}, S_j^{\{i\}}) - g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{\{i\}}) \dots\dots\dots\mathscr{E}_j^{\{i\}} \\
&- \left(g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{\{i\}}) - g_j(\mathbf{E}_j^*, C^{\{i\}}, S_j^{\{i\}}) \right) \dots\dots\dots -\mathscr{C}_j^{\{i\}} \\
&\left[\begin{array}{l} + \left(g_j(\mathbf{E}_j, C^{\{i\}}, S_j^{\{i\}}) - g_j(\mathbf{E}_j^*, C^{\{i\}}, S_j^{\{i\}}) \right) \\ - \left(g_j(\mathbf{E}_j, C^{*\{i\}}, S_j^{\{i\}}) - g_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{\{i\}}) \right) \end{array} \right] \dots\dots\mathscr{I}_j^{\{i\}}
\end{aligned} \qquad \text{A.14}$$

where the quantity $\bar{r}_i{'}$ measures mean fitness, the curly quantity are standard parameters measuring the effect of E, C, S and their interactions in the unit of population growth rate. The quantity $\mathscr{S}$ measure the effect of structure in population growth rate; the quantity $\mathscr{E}$ is the effect of environment; the quantity $\mathscr{C}$ measures the effect of competition; the quantify $\mathscr{I}$ is the effect of interaction between environment and competition.

Averaging the growth rate over time we have the long-term recovery rate

for invader

$$\bar{r}_i = \bar{r}_i{'} + S_i + E_i - C_i + I_i \qquad \text{A.15}$$

and for resident

$$\overline{r}_r = \overline{r}_r' + S_r + E_r + I_r = 0 \qquad\qquad \text{A.16}$$

where S, E and I are $E[\mathcal{S}]$, $E[\mathcal{E}]$ and $E[\mathcal{I}]$ respectively.

The resident long-term recovery rate $\overline{r}_r$ is zero because its population converges on stationary fluctuation. We rearrange A.15 as invader-resident comparisons

$$
\begin{aligned}
\overline{r}_i &= \overline{r}_i - \overline{r}_r \\
&= \overline{r}_i' - \overline{r}_r' + \underbrace{S_i - S_r}_{\Delta S_i} + \underbrace{E_i - E_r}_{\Delta E_i} - \underbrace{(C_i - C_r)}_{\Delta C_i} + \underbrace{I_i - I_r}_{\Delta I_i} \\
&= \Delta S_i + \Delta E_i - \Delta C_i + \Delta I_i
\end{aligned}
\qquad\qquad \text{A.17}
$$

We can omit $\overline{r}_i' - \overline{r}_r'$ as it is 0 due to because our special assumption that two species have equal fitness in equilibrium $\overline{r}_i' = \overline{r}_r'$.

Approximation for mean effect of structure (ΔS_i)

The mean effect of structure can be approximated as effect of shift in mean structure:

$$
\begin{aligned}
\Delta S_i &= E\left[\begin{array}{l}\left(g_i(\mathbf{E}_i^*, C_i^{*\{r\}}, S_i) - g_i(\mathbf{E}_i^*, C_i^{*\{r\}}, S_i^{*\{r\}})\right) \\ -\left(g_r(\mathbf{E}_r^*, C_r^{*\{r\}}, S_r) - g_r(\mathbf{E}_r^*, C_r^{*\{r\}}, S_r^{*\{r\}})\right)\end{array}\right] \\
&= E\left[g_i(\mathbf{E}_i^*, C_i^{*\{r\}}, S_i) - g_r(\mathbf{E}_r^*, C_r^{*\{r\}}, S_r)\right] \\
&\approx \ln E\left[G_i(\mathbf{E}_i^*, C_i^{*\{r\}}, S_i)\right] - \ln E\left[G_r(\mathbf{E}_r^*, C_r^{*\{r\}}, S_r)\right] \\
&= g_i\left(\mathbf{E}_i^*, C_i^{*\{r\}}, E[S_i]\right) - g_r\left(\mathbf{E}_r^*, C_r^{*\{r\}}, E[S_r]\right)
\end{aligned}
\qquad \text{A.18}
$$

The approximation applies if nonlinearities in structure are not large for the range of variation in structure that occurs. The adequacy of this approximation for the cases considered here was confirmed by simulation.

Approximation for mean environment effect (ΔE_i)

The mean environment effect can be approximated as

$$\Delta E_i = E[\mathscr{C}_i^{\{i\}} - \mathscr{C}_r^{\{i\}}]$$

$$= E\begin{bmatrix} \left(g_i(\mathbf{E}_i, C^{*\{i\}}, S_i^{\{i\}}) - g_i(\mathbf{E}_i^*, C^{*\{i\}}, S_i^{\{i\}}) \right) \\ -\left(g_r(\mathbf{E}_r, C^{*\{i\}}, S_r^{\{i\}}) - g_r(\mathbf{E}_r^*, C^{*\{i\}}, S_r^{\{i\}}) \right) \end{bmatrix}$$

$$\approx \left(\ln E\left[G_i(\mathbf{E}_i, C^{*\{i\}}, S_i^{\{i\}}) \right] - \ln E\left[G_i(\mathbf{E}_i^*, C^{*\{i\}}, S_i^{\{i\}}) \right] \right)$$

$$- \left(\ln E\left[G_r(\mathbf{E}_r, C^{*\{i\}}, S_r^{\{i\}}) \right] - \ln E\left[G_r(\mathbf{E}_r^*, C^{*\{i\}}, S_r^{\{i\}}) \right] \right) \qquad \text{A.19}$$

if nonlinearities in environment and structure are not large for the range of variation

occurs.

The finite rate of increase G are additive in components from survival G_s, seedling

recruitment G_b, seedling growth G_{bg}, and post recruitment individual growth G_g (Table

A.2 Yuan and Chesson, in progress).

We define following mean finite rate of increase as

$$E\left[G_j(\mathbf{E}_j^*, C^{*\{i\}}, S_j^{\{i\}}) \right] = G_{js} + G_{jb} + G_{jbg} + G_{jg} \qquad \text{A.20}$$

where $j = i$ or r.

Then $E\left[G_j(\mathbf{E}_j, C^{*\{i\}}, S_j^{\{i\}}) \right]$ can be represented using G_j giving e^E in Eq.2 follows

lognormal distribution, and there is no covariance between $\mathbf{E}$ and S:

$$E\left[G_j(\mathbf{E}_j, C^{*\{i\}}, S_j^{\{i\}}) \right] = G_{js} + G_{jb}e^{\sigma_{jb}^2/2} + G_{jbg}e^{\left(\sigma_{jb}^2 + \sigma_{jg}^2\right)/2 + \sigma_{jbg}} + G_{jg}e^{\sigma_{jg}^2/2}. \text{ A.21}$$

We also define the p values as the fraction of different components of finite rate of

increases: $p_{js}=G_{js}/G_j$, $p_{jb}=G_{jb}/G_j$, $p_{jbg}=G_{jbg}/G_j$, and $p_{jg}=G_{jg}/G_j$.

Thus A.19 can be expressed in p's as:

$$\Delta E_i \approx \ln\left(\frac{p_{ibg}e^{\left(\sigma_{ib}^2 + \sigma_{ig}^2 + 2\sigma_{ibg}\right)/2} + p_{ig}e^{\sigma_{ig}^2/2} + p_{ib}e^{\sigma_{ib}^2/2} + p_{is}}{p_{rbg}e^{\left(\sigma_{rb}^2 + \sigma_{rg}^2 + 2\sigma_{rbg}\right)/2} + p_{rg}e^{\sigma_{rg}^2/2} + p_{rb}e^{\sigma_{rb}^2/2} + p_{rs}} \right). \qquad \text{A.22}$$

Because we assume there is no correlation within species between environmental response in reproduction and environmental response in growth $\sigma_{bg} = 0$, this expression can be simplified as Eq 7:

$$\Delta E_i \approx \ln\left(\frac{p_{ibg}e^{\left(\sigma_{ib}^2 + \sigma_{ig}^2\right)/2} + p_{ig}e^{\sigma_{ig}^2/2} + p_{ib}e^{\sigma_{ib}^2/2} + p_{is}}{p_{rbg}e^{\left(\sigma_{rb}^2 + \sigma_{rg}^2\right)/2} + p_{rg}e^{\sigma_{rg}^2/2} + p_{rb}e^{\sigma_{rb}^2/2} + p_{rs}} \right). \qquad 7$$

Approximation for the storage effect (ΔI_i)

Two forms of the storage effect can arise, one due to reproduction (ΔI_{ib}) and one due to growth (ΔI_{ig}). The storage effect are measured as differences in covariance between environment and competition (covEC) between invader and resident weighted by buffer in their population growth. The approximation for buffer, as measured by storage coefficient ψ, and covEC, χ, can be found in detail in (Yuan and Chesson, in progress) so we will not repeat here. The following are full expression for the storage effect in reproduction and storage effect in growth in general cases where species can be correlated.

Storage effect due to reproduction

$$\Delta I_b \approx \gamma_{ib} \chi_{ib} - \gamma_{rb} \chi_{rb}$$

$$\approx \frac{-\left(p_{ib} + p_{ibg}\right) p_{is}}{1 - p_{is}} \left(\theta_{rg} \operatorname{cov}(E_{bi}, E_{gr}) + \theta_{rb} \operatorname{cov}(E_{bi}, E_{br})\right)$$

$$+ \frac{\left(p_{rb} + p_{rbg}\right) p_{rs}}{1 - p_{rs}} \left(\theta_{rg} \operatorname{cov}(E_{br}, E_{gr}) + \theta_{rb} \operatorname{var}(E_{br})\right) \qquad \text{A. 23}$$

$$= \frac{-\left(p_{ib} + p_{ibg}\right) p_{is}}{1 - p_{is}} \left(\theta_{rg} \sigma_{b_i g_r} + \theta_{rb} \sigma_{b_i b_r}\right)$$

$$+ \frac{\left(p_{rb} + p_{rbg}\right) p_{rs}}{1 - p_{rs}} \left(\theta_{rg} \sigma_{b g_r} + \theta_{rb} \sigma_{b b_r}\right)$$

Storage effect due to growth

$$\Delta I_g \approx \gamma_{ig} \chi_{ig} - \gamma_{rg} \chi_{rg}$$

$$\approx \frac{-\left(p_{ig} + p_{ibg}\right) p_{is}}{1 - p_{is}} \left(\theta_{rg} \operatorname{cov}\left(E_{gi}, E_{gr}\right) + \theta_{rb} \operatorname{cov}\left(E_{gi}, E_{br}\right)\right)$$

$$+ \frac{\left(p_{rg} + p_{rbg}\right) p_{rs}}{1 - p_{rs}} \left(\theta_{rg} \operatorname{var}\left(E_{gr}\right) + \theta_{rb} \operatorname{cov}\left(E_{gr}, E_{br}\right)\right) \qquad \text{A. 24}$$

$$= \frac{-\left(p_{ig} + p_{ibg}\right) p_{is}}{1 - p_{is}} \left(\theta_{rg} \sigma_{g_i g_r} + \theta_{rb} \sigma_{g_i b_r}\right)$$

$$+ \frac{\left(p_{rg} + p_{rbg}\right) p_{rs}}{1 - p_{rs}} \left(\theta_{rg} \sigma_{g_{rr}} + \theta_{rb} \sigma_{g_r b_r}\right)$$

Appendix III

Fecundity schedule

The fecundity of an individual partly depends on a species specific size-dependent fecundity schedule. The fecundity schedule in this study is specified as species-specific linear function of size, a_{jc}, with slope κ_{j1} and size threshold a_{j0}:

$$k_{j,a_{jc}} = \max(\kappa_{j1}(a_{jc} - a_{j0}), 0). \qquad \text{A. 25}$$

The specific values chosen for κ_{j1} and a_{j0} are listed in Table A.2.

Mortality schedule

Mortality rate of any individual is determined by a species-specific mortality schedule specified by five parameters:

$$m_{a_{jc}} = \frac{m_0 e^{-\alpha_d a_{jc}^2} + m_m e^{-\alpha_d (a_{jc}-a_m)^2} + m_\infty (1 - e^{-\alpha_d a_{jc}^2})}{1 + e^{-\alpha_d (a_{jc}-a_m)^2}} \qquad \text{A.26}$$

The parameters m_0, m_m and m_∞ specify that the mortality is near m_0 at small sizes, decreases towards m_m as sizes increases, and increase towards m_∞ as size is very large. The parameter α_d determines how rapid mortality rate moves between these different levels with size. The parameter a_m determines the size after which mortality rate increase with size. The parameters α_d and a_m are fixed in all cases as 0.05 and 10 respectively. The values chosen for m_0, m_m and m_∞ are listed in Table A.2.

Growth schedule, also called competitiveness schedule

In this study we choose a Gompertz-alike function for growth schedule so that in equilibrium cases, tree size increase slowly when small, faster when tree gets larger, slows down and stop growing eventually when tree get very large (Fig. 2c).

The original Gompertz growth function is for differential equation model where the growth of tree follow the following equation

$$\frac{dy}{dt} = b_0 - b_1 y \qquad \text{A.27}$$

where $y = \ln a$, the logarithm of tree size a.

We adapted Eq. A.27 for the competitiveness schedule of the trees that will produce similar shapes of schedules:

$$c_{j,a_{jc}} = \max\left(a_{jc}(\beta_{j,.1} - \beta_{j,2} \ln(a_{jc})), 0\right) \qquad \text{A.28}$$

The values chosen for β_0 and β_1 are listed in Table A.2.

Gradient of tradeoff

Parameters for the demographic schedules are chosen to enforce tradeoff between fecundity and growth schedules. At the extreme of the tradeoff, the species have mean advantage in fecundity have fecundity contribute primarily to population growth; the species have mean advantage in growth have growth contribute primarily to population growth. Parameters (Table A.2) are chosen through the numerical solution (eqSolve in Gauss 14, Aptech inc.) so that species can coexist neutrally in constant environment. We label the fecundity schedules and competitive at the strong asymmetric end of the tradeoff with *: $k^*_{j,a_{jc}}$ and $c^*_{j,a_{jc}}$. We morph the schedules between two species to create a continuous gradient of the tradeoff by varying the weights p between $[0,0.5]$. So that one species has fecundity schedule as

$$k_{1,a_{1c}} = (1-p)k^*_{1,a_{1c}} + pk^*_{2,a_{2c}} \quad (1.1)$$
<div align="right">A. 29</div>

and its competitor has fecundity schedule as

$$k_{2,a_{2c}} = pk^*_{1,a_{1c}} + (1-p)k^*_{2,a_{2c}} \quad . (1.2)$$
<div align="right">A.30</div>

The competitive schedules are morphed in similar way but with a different weights p'. The weight p' is solved numerically using the same method (eqSolve in Gauss) so species can coexist neutrally in constant environment. It also falls in the range $[0, 0.5]$. One species have competitive schedule as

$$c_{1,a_{1c}} = (1-p')c^*_{1,a_{1c}} + p'c^*_{2,a_{2c}}$$
<div align="right">A.31</div>

and its competitor has fecundity schedule as

$$c_{2,a_{1c}} = p'c^*_{1,a_{1c}} + (1-p')c^*_{2,a_{2c}} \quad .$$
<div align="right">A. 32</div>

Comparisons between different shapes of demographic processes

When we used flat cases as a reference point, we kept the relative mean importance of reproduction, individual growth, and survival, as close as possible to cases at the extreme end of the tradeoff. That way, p's are relative constant, we will be mainly investigating the effect of shapes. To achieve such goal, we kept the single species steady state life-time fecundity, the longevity, the life-time average competitiveness identical between the two scenarios. These life-time average demographic traits, where the constraints are applied, are calculated by averages weighted by the stationary age structure. To calculate these age-averaged demographic traits, it is necessary to obtain the age dependency in demographic schedules. In equilibrium cases, there is a one-to-one correspondence between age structure and size structure. We know the demographic trait for individuals at certain age by first figuring out their size at different ages. Under single species steady state, an individual grow at fix rate, and there is a unique projection between the size structure and the age structure. The size of individual at age x is obtained by iteration through the following process in single species steady state:

$$
\begin{aligned}
a_j(x) &= a_j(x-1) + c_{a_j(x-1)} e^{\mu_{gj} - C^*} \\
a_j(x-1) &= a_j(x-2) + c_{a_j(x-2)} e^{\mu_{gj} - C^*} \\
&\ldots \\
a_j(2) &= a_j(1) + c_{a_j(1)} e^{\mu_{gj} - C^*}
\end{aligned}
\qquad . \qquad \text{A. 33}
$$

$a_j(x)$ is defined as the size of individual at age $\underline{x}$, and the size of individual at age 1 is defined as the size of the initial seedling cohort $a_j(1) = a_{js}$. The variable μ_{gj} is the mean environmental responses in growth and C^* is the constant competitive responses in single species steady state. After knowing their sizes at different ages, we could obtain the age-

structured demographic schedule. For individual of age x from species j, we label its

fecundity rate as $k_j(x)$ where $k_j(x) = k_{a_j(x)}$, its mortality rate as $m_j(x)$ where $m_j(x) = m_{a_j(x)}$

, and its competitiveness as $c_j(x)$ where $c_j(x) = c_{a_j(x)}$.

The probability that an individual of species j survives to age x is l_{jx} where

$$l_{jx} = \Pi_{i=1}^{x-1}(1 - m_j(i)).$$ A.34

Due to the fixed growth rate under single species steady state, only certain sizes are

possible, which make the model similar to an age-structured matrix model. Many well-

studied properties of the matrix model can be applied. The stationary age distribution is

$$\pi_{jx} = \frac{l_{jx}}{\sum_{x=1}^{\infty} l_x}$$ A.35

The stationary age distribution is used as a weight to calculate average demographic

traits. For the purpose of comparing different fecundity schedules, we fixed the average

fecundity, weighted by the stationary age structure in Eq A.35 , under single species

steady state:

$$\overline{k_j} = e^{\mu_{bj}} \frac{\sum_{x=1}^{\infty} k_{jx}(x)l_{jx}}{\sum_{x=1}^{\infty} l_{jx}}$$ A.36

where μ_{bj} is the mean environmental responses in reproduction.

For mortality schedules, we fixed the average life-span under single species steady state.

The life span for individual in structured population is estimated as:

$$L_j = \sum_{x=1}^{\infty} l_{jx}.$$ A.37

For the purpose of comparing different competitiveness schedule, we fixed the average

competitiveness weighted by the stationary age structure under single species steady

state:

$$\overline{c}_j = e^{\mu_{gj}} \frac{\sum\limits_{x=1}^{\infty} c_{jx}(x) l_{jx}}{\sum\limits_{x=1}^{\infty} l_{jx}} \qquad\qquad A.38$$

Table A.2 Parameters of demographic schedules

Cases ⟍ Schedules		Fecundity schedule	Mortality schedule	Competitiveness schedule
Strongly asymmetric end for Fig. 1-6	Species with mean advantage in reproduction (sp1)	$\kappa_{11} = 2.178$ $a_{10} = 0, \mu_{1b} = 1$	$m_0 = 0.1$ $m_m = 0$ $m_\infty = 0.02$	$\beta_{1,1} = 0.03$ $\beta_{1,2} = 0.01, \mu_{1g} = 1$
	Species with mean advantage in growth (sp2)	$\kappa_{11} = 0.5$ $a_{10} = 1, \mu_{1b} = 1$		$\beta_{2,1} = 0.3$ $\beta_{2,2} = 0.05, \mu_{2g} = 1$
Fig. 7	Species with mean advantage in reproduction (sp1)	$k_1 = 0.421$	m=0.020	$\beta_{1,1} = 0.03$ $\beta_{1,2} = 0.01, \mu_{1g} = 1$
	Species with mean advantage in growth (sp2)	$K_2 = 0.401$	m=0.019	$\beta_{2,1} = 0.3$ $\beta_{2,2} = 0.05, \mu_{2g} = 1$

References:

Baker, T. R., M. D. Swaine, and D. Burslem. 2003. Variation in tropical forest growth rates:

combined effects of functional group composition and resource availability. Perspectives

in Plant Ecology Evolution and Systematics **6**:21-36.

Chesson, P. 1994. Multispecies competition in variable environments. Theoretical population biology **45**:227-276.

Chesson, P., N. J. Huntly, S. H. Roxburgh, M. Pantastico-caldas, and J. M. Facelli. 2013. The storage effect: definition and tests in two plant communities

Temporal Dynamics and Ecological Process. Cambridge University Press.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**:343-366.

Chesson, P. L. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical population biology **64**:345-357.

Chesson, P. L. 2008. Quantifying and testing species coexistence mechanisms. Unity in Diversity: Reflections on Ecology after the legacy of ramon margelef.

Clark, D. A. and D. B. Clark. 1992. Life-history diversity of canopy and emergent trees in a neotropical rain-forest. Ecological Monographs **62**:315-344.

Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. Gunatilleke, C. V. S. Gunatilleke, P. Hall, K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. LaFrankie, S. L. de Lao, J. R. Makana, M. N. S. Noor, A. R. Kassim, S. Russo, R. Sukumar, C. Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa, and T. Zillio. 2006. The importance of demographic niches to tree diversity. Science **313**:98-101.

Esther, A., J. Groeneveld, N. Enright, B. Miller, B. Lamont, G. W. Perry, B. Tietjen, and F. Jeltsch. 2011. Low-dimensional trade-offs fail to explain richness and structure in species-rich plant communities. Theoretical Ecology **4**:495-511.

Gilbert, B., S. J. Wright, H. C. Muller-Landau, K. Kitajima, and A. Hernandez. 2006. Life history trade-offs in tropical trees and lianas. Ecology **87**:1281-1288.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Iida, Y., T. S. Kohyama, T. Kubo, A. Kassim, L. Poorter, F. Sterck, and M. D. Potts. 2011. Tree architecture and life-history strategies across 200 co-occurring tropical tree species. Functional Ecology **25**:1260-1268.

Iida, Y., L. Poorter, F. J. Sterck, A. R. Kassim, M. D. Potts, T. Kubo, and T. Kohyama. 2013. Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. Ecology.

Jakobsson, A. and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. Oikos **88**:494-502.

Kelly, C. K. and M. G. Bowler. 2002. Coexistence and relative abundance in forest trees. Nature **417**:437-440.

Kelly, C. K. and M. E. Hanley. 2005. Juvenile growth and palatability in co-occurring, congeneric British herbs. American Journal of Botany **92**:1586-1589.

Kelly, D. and V. L. Sork. 2002. MAST SEEDING IN PERENNIAL PLANTS: Why, How, Where? Annual Review of Ecology and Systematics **33**:427-447.

Kimball, S., J. R. Gremer, A. L. Angert, T. E. Huxman, and D. L. Venable. 2012. Fitness and physiology in a variable environment. Oecologia **169**:319-329.

Kneitel, J. M. and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters **7**:69-80.

Kobe, R. K. 1999. LIGHT GRADIENT PARTITIONING AMONG TROPICAL TREE SPECIES THROUGH DIFFERENTIAL SEEDLING MORTALITY AND GROWTH. Ecology **80**:187-201.

Lusk, C. H. and B. Smith. 1998. LIFE HISTORY DIFFERENCES AND TREE SPECIES COEXISTENCE IN AN OLD-GROWTH NEW ZEALAND RAIN FOREST. Ecology **79**:795-806.

McMahon, S. M., C. J. E. Metcalf, and C. W. Woodall. 2011. High-Dimensional Coexistence of Temperate Tree Species: Functional Traits, Demographic Rates, Life-History Stages, and Their Physical Context. Plos One **6**.

Nakashizuka, T. 2001. Species coexistence in temperate, mixed deciduous forests. Trends in Ecology & Evolution **16**:205-210.

Ostling, A. 2012. Do fitness-equalizing tradeoffs lead to neutral communities? Theoretical Ecology **5**:181-194.

Ouedraogo, D. Y., F. Mortier, S. Gourlet-Fleury, V. Freycon, and N. Picard. 2013. Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa. Journal of Ecology **101**:1459-1470.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press Oxford.

Turelli, M. 1981. Niche overlap and invasion of competitors in random environments I: models without demographic stochasticity Theoretical Population Biology **20**:1-56.

Turnbull, L. A., M. Rees, and M. J. Crawley. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. Journal of Ecology **87**:899-912.

Turnbull, L. A., M. Rees, and D. W. Purves. 2008. Why equalising trade-offs aren't always neutral. Ecology Letters **11**:1037-1046.

Vincent, G., H. de Foresta, and R. Mulia. 2009. Co-occurring tree species show contrasting sensitivity to ENSO-related droughts in planted dipterocarp forests. Forest Ecology and Management **258**:1316-1322.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125-159.

Wright, S., H. Muller-Landau, O. Calderon, and A. Hernandez. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology **86**:848-860.

Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Díaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology **91**:3664-3674.

Yuan, C. and P. Chesson. , in progress. A structured lottery model for species coexistence in a variable environment: general coexistence mechanisms for species with complex life histories.

Yuan, C. and P. Chesson. In review. The relative importance of relative nonlinearity in the lottery model. Theoretical population biology.