UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS

Variabilidad climática y mantenimiento de la diversidad vegetal en un pastizal rico en especies

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

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Índice

Resumen

Debido al actual escenario de cambio climático, se espera que la variabilidad temporal aumente considerablemente. Sin embargo, sus efectos sobre el mantenimiento de la diversidad no son concluyentes. A pesar del fuerte desarrollo teórico, la evidencia respecto a la contribución relativa de los diferentes mecanismos a la coexistencia de especies aún es escasa, en particular de los mecanismos dependientes de las fluctuaciones. Estos proveen información del efecto de las fluctuaciones temporales sobre la coexistencia de especies y, en consecuencia, de los efectos que la variabilidad climática pudiera ejercer sobre la diversidad de especies. Un enfoque cuantitativo del estudio de los diferentes mecanismos de coexistencia permitiría relacionar sus contribuciones relativas a la coexistencia con aquellos factores que la subyacen. En este estudio se pretende evaluar el efecto de las fluctuaciones temporales, la distancia filogenética y de algunos atributos de historias de vida sobre el mantenimiento de la diversidad vegetal en un pastizal semiárido.

En el capítulo I, se cuantificó la contribución relativa de diferentes mecanismos a la coexistencia de 19 especies de plantas. Se utilizó una serie de 13 años de datos para parametrizar un modelo poblacional para cada especie y posteriormente se hicieron análisis de invasibilidad para desagregar cada mecanismo de coexistencia. Se encontró que 17 de las 19 especies tuvieron potencial para coexistir de manera estable. La diferenciación de nicho independiente de las fluctuaciones fue el mecanismo con mayor contribución a la coexistencia, seguido de la no linealidad relativa. Mientras que las contribuciones del efecto de almacenamiento fueron casi nulas o negativas.

En el capítulo II se estudió el papel de la distancia filogenética sobre el mantenimiento de la diversidad. Se analizó la magnitud de la competencia por pares de especies, la sincronicidad

(grado de correlación entre las respuestas demográficas de las especies) y los ingredientes del efecto de almacenamiento respecto a la distancia filogenética. También se evaluó el efecto de la riqueza de especies y la distancia filogenética en los tres mecanismos de coexistencia estable. Finalmente, se evaluó el efecto de la sincronicidad sobre la coexistencia, simulando comunidades en las cuales todas las especies tienen respuestas idénticas o completamente aleatorias a las fluctuaciones ambientales. La contribución de la diferenciación de nicho independiente de las fluctuaciones fue mayor entre especies lejanamente emparentadas debido a que la competencia entre ellas es más débil. Las especies cercanamente emparentadas fueron más sincrónicas, afectando negativamente al efecto de almacenamiento. La no linealidad relativa fue más importante en ambos extremos del gradiente filogenético pero no en el centro, quizás como resultado de diferentes respuestas no lineales a la competencia entre especies lejanamente emparentadas y a la sincronicidad entre parientes cercanos. El efecto de la distancia filogenética fue despreciable entre pares de especies, pero sus efectos parecen ser más relevantes mientras más especies se encuentren interactuando, lo que sugiere que las relaciones de parentesco podrían ser importantes en comunidades altamente diversas.

En el capítulo III, se evaluó la hipótesis de que los bancos de semillas y la longevidad de los individuos establecidos amortiguan los efectos de la competencia en los años adversos. Para caracterizar los bancos de semillas de las 19 especies de estudio, se realizó un experimento de supervivencia de semillas en el suelo en campo y se tomaron muestras de suelo. También se siguió el crecimiento y la supervivencia de nueve especies perennes durante cinco años para calcular la esperanza de vida. Posteriormente, estos datos se correlacionaron con el potencial de las especies para amortiguar la competencia. Se encontró que los individuos más longevos tienen mayor potencial de amortiguamiento, pero sólo aquellos que se encuentran establecidos y no en los bancos de semillas.

Abstract

Strong climate variability characterizes many regions of the world and this variability is expected to keep growing. Despite the advances in ecological theory, evidence for the relative importance of the different mechanisms that promote species coexistence is lacking, in particular, for those mechanisms that depend on temporal fluctuations. However, the effect of increased climate variability on species diversity depends on the role of temporal fluctuations in regulating species coexistence. Moreover, little is known about how different factors may affect the strength of the different coexistence mechanisms that promote stable coexistence. In this work, I aim to assess how temporal fluctuations, evolutionary relatedness of the species, and some life-history traits affect species diversity.

In chapter I, I quantified the relative contribution of different mechanisms to the coexistence of 19 species by using field-parameterized population models and invasion analysis. Results showed that 17 out of 19 species had the potential to coexist stably. Species diversity was mainly maintained by large fluctuation-independent niche differences. Relative nonlinearity was the second mechanism that contributed the most to species coexistence and it also increased the fitness of species that were less favored by fluctuation-independent niche differentiation. The storage effect was negligible or destabilizing.

In chapter II, I studied the role of phylogenetic distance on diversity maintenance. Here, I analyzed how pairwise competition, synchronicity (similar demographic responses over time) and storage effect ingredients depend on phylogenetic distance. Then, I assessed the effects of phylogenetic distance and species richness on the three stable coexistence mechanisms. Finally, I analyzed how synchronicity affects coexistence by simulating communities in which all the species have identical or uncorrelated responses to environmental fluctuations. As expected,

stabilization through fluctuation-independent niche differentiation was stronger between distant relatives because of weaker competition. Synchronicity was higher between close relatives, with negative effects on the contribution of the storage effect to coexistence. The relative nonlinearity was strong at both ends of the phylogenetic gradient but not in the middle, which may result from different nonlinear responses to competition between distant relatives and stronger fluctuations in competition due to synchronicity between closer relatives. The effect of phylogenetic distance on coexistence was almost negligible when pairwise species were analyzed, but it became stronger as more species interacted, suggesting that evolutionary relatedness may be influential in species-rich communities.

In chapter III, I tested the hypothesis that seed banks and individual longevity buffer competition in adverse years. A seed survival experiment was conducted in a semiarid grassland and soil samples were taken to characterize the seed banks of the 19 species of forbs and grasses. Also, the survival and growth of nine perennial species were followed for five years to calculate their mean life expectancy. Next, those data were correlated with the capacity of species to buffer competition. Evidence showed that mean life expectancy, but not seed banks, was positively related to species' capacity to buffer competition but not seed banks. These results highlight the importance of determining the specific features of the species traits related to species' ability to buffer population growth against the negative effects of unfavourable environmental and competitive conditions to understand better how the storage effect promotes or precludes stable coexistence.

Introducción general

La variabilidad climática caracteriza a todos los ecosistemas del mundo (Adler *et al.* 2006) . Debido al cambio climático, se prevé que en muchas regiones esta variabilidad aumente, trayendo consigo un incremento en la frecuencia de tormentas severas y sequías (Karl y Trenberth 2003; Salinger 2005). Actualmente se tiene un gran cuerpo teórico que examina los efectos de las fluctuaciones ambientales en la coexistencia de especies (Chesson 2000b). Sin embargo, la evidencia empírica aún es escasa.

Entender los efectos de las fluctuaciones ambientales sobre la persistencia de las poblaciones y las interacciones entre individuos de una misma comunidad es de vital importancia para predecir los impactos ecológicos del cambio climático (Adler y Drake 2008). La evidencia empírica que aportan los análisis de viabilidad poblacional, sugiere que la variabilidad ambiental incrementa el riesgo de extinción de las especies, en parte, debido a la alta sincronía espacial de las especies con áreas de distribución restringidas (Boyce 1992; Menges y Quintana-Ascencio 2000). Por otro lado, hay un gran cuerpo teórico que enfatiza que la variabilidad ambiental provee nuevas formas en las que las especies se pueden diferenciar ecológicamente, reduciendo así las interacciones con otros miembros del mismo gremio (Chesson 1983a; Chesson 1994, 2000b; Chesson *et al.* 2004). Esto puede resolver la contradicción entre la teoría ecológica clásica, que sostiene que la competencia por los mismos recursos debería llevar a la extinción a la mayoría de las especies excepto a las mejores competidoras (Tilman 1982), y la gran diversidad de especies que se pueden encontrar en varias comunidades en diferentes partes del mundo.

Teoría moderna de la coexistencia

Históricamente, hay dos hipótesis que han permeado fuertemente la manera en la que se ha estudiado la coexistencia de especies: una plantea que las especies compiten por el espacio pero son ecológicamente idénticas y por lo tanto tienen la misma adecuación bajo todas las condiciones, resultando en la dominancia de una especie debido a procesos aleatorios; la teoría neutral de la biodiversidad (Hubbell 2001) y otra, que plantea que la diferenciación de nichos entre las especies es lo que permite su coexistencia; la teoría de la exclusión competitiva (Gause 1934). En contraste, la teoría moderna de la coexistencia (Chesson 2000b) plantea que la persistencia indefinida de las especies en una comunidad resulta del balance entre los efectos igualadores, los cuales emergen cuando las especies son ecológicamente semejantes en sus tasas vitales y por lo tanto tienen la misma adecuación; y los efectos estabilizadores, en donde la diferenciación de nichos permite la coexistencia de especies en condiciones estables (Chesson 2000b).

Los mecanismos igualadores no estabilizan la coexistencia ya que una vez que haya diferencias en la adecuación, disminuirá la densidad de las especies menos favorecidas, llegando eventualmente a la extinción (Chesson 2000b). Mientras que, en los mecanismos de coexistencia estable, si las densidades de las especies disminuyen éstas eventualmente se pueden recuperar (Chesson 2000b).

La diferenciación de nichos promueve la coexistencia estable entre las especies. Cuando la competencia intraespecífica es más intensa que la competencia interespecífica, las especies pueden limitarse a sí mismas a tráves de regulación dependiente de la densidad (Chesson 1994, 2000b). Esto significa que las especies pueden autorregular sus poblaciones, evitando el crecimiento exponencial y dejando disponibles los recursos para otras especies de la misma comunidad. Además, asegura que los efectos negativos de la competencia interespecífica no sean tan fuertes como para llevar a la especie a la extinción. De acuerdo con la teoría moderna de la coexistencia, la diferenciación de nichos puede ser independiente o dependiente de las fluctuaciones (Chesson 1994, 2000b).

La diferenciación de nichos independiente de las fluctuaciones comprende a los mecanismos que operan en un tiempo y espacio determinado (Chesson *et al.* 1990). Los ejemplos más comunes de estos mecanismos son la depredación dependiente de la frecuencia y la diferenciación de recursos o depredadores (Chesson *et al.* 1990; Chesson 2000b). Estos mecanismos promueven la coexistencia estable porque cuando una especie se encuentra a muy bajas densidades, ésta puede aprovechar los beneficios de una menor competencia intraespecífica y así poder aumentar sus tamaños poblacionales (Chesson 2000a).

Para la mayoría de las especies, los cambios en las condiciones ambientales podrían provocar fluctuaciones en las tasas de natalidad, supervivencia, germinación, fecundidad, u otros parámetros poblacionales de una época de reproducción a la siguiente (Warner y Chesson 1985). Estas fluctuaciones podrían promover el mantenimiento de la diversidad de las especies de una comunidad a través del efecto de almacenamiento y/o la no linealidad relativa (Chesson 2000b, a, 2003).

El efecto de almacenamiento debe su nombre a que en épocas favorables, en las que se reclutan una gran cantidad de individuos, éstos pueden mantenerse en la población (se almacenan) durante épocas desfavorables para posteriormente contribuir al crecimiento poblacional una vez que las condiciones se tornen benignas (Chesson y Huntly 1988). Estos modelos plantean que las especies que se encuentran en una misma comunidad se benefician en diferentes tipos de condiciones y almacenan los beneficios de años favorables (por ejemplo, la permanencia de los individuos o los bancos de semillas en especies de plantas) para aminorar los efectos de la competencia en años o condiciones desfavorables (Levine y Rees 2004). Sin embargo, para que el efecto de almacenamiento pueda estabilizar la coexistencia se deben cumplir tres condiciones: 1) Diferentes respuestas al ambiente: Las especies de una misma comunidad tendrán diferentes desempeños demográficos bajo las mismas condiciones ambientales. El desacoplamiento demográfico entre especies permitiría que puedan incrementarse las tasas de crecimiento de las especies que se encuentren en bajas densidades, evitando así la exclusión competitiva (Chesson 1994, 2000a). 2) Covarianza clima-competencia: Esto es una medida de qué tan afectada se ve una especie por la competencia (Chesson 2018). En años favorables, se esperaría que la competencia fuera más intensa (Ellner *et al.* 2016). Mientras que en los años desfavorables en los que la especie se encuentra a bajas densidades, se esperaría que ésta no se vea afectada positiva o negativamente por la competencia para que la especie pueda tomar ventaja de las condiciones favorables para aumentar su densidad (Ellner *et al.* 2016). 3) Amortiguamiento o subaditividad: Para que las especies puedan persistir ante periodos adversos, cuando los recursos son limitados y las tasas de reclutamiento son bajas o incluso nulas, se esperaría que el efecto de la competencia sea mucho menor en épocas desfavorables comparado con las épocas favorables, de manera que las densidades poblacionales no declinen bruscamente hasta extinguirse (Chesson y Huntly 1988).

La no linealidad relativa promueve la coexistencia estable de especies cuando las especies que componen una comunidad presentan diferentes respuestas no lineares a la competencia (Yuan y Chesson 2015). Esto significa que las especies se verán afectadas de diferentes maneras por las fluctuaciones o cambios en la intensidad de la competencia y ninguna se verá favorecida o afectada negativamente en todos los niveles de competencia. Para que la no linealidad relativa promueva la coexistencia estable de especies, las especies deben diferir en la curvatura de sus respuestas a la competencia (Yuan y Chesson 2015; Chesson 2018). De manera que, una especie crecerá mejor bajo condiciones competitivas promedio, mientras que la otra tendrá un mejor desempeño bajo condiciones competitivas variables. Esto permite que la especie que no se beneficia de las condiciones promedio pueda aprovechar las fluctuaciones en la competencia para aumentar su tasa de crecimiento poblacional y evitar la extinción.

Consecuencias de algunos atributos de historias de vida sobre la coexistencia de especies

Las zonas áridas son sistemas ideales para probar los efectos de la variabilidad sobre la coexistencia debido a las fluctuaciones en la precipitación (Chesson *et al.* 2004). En dichas zonas, se observan cambios anuales en la composición de las comunidades vegetales (Pake y Venable 1995; Guo y Brown 1996), lo que sugiere que las especies responden de modo diferencial a la variabilidad ambiental (Pake y Venable 1995, 1996; Facelli *et al.* 2005). En estos ecosistemas, la variabilidad en la precipitación, tanto espacial como temporal, determina la cantidad de agua disponible para los diferentes tipos de plantas (Chesson y Huntly 1993).

Al haber fluctuaciones en la disponibilidad de recursos, la abundancia de especies y densidad de individuos también va a fluctuar y en consecuencia se esperaría que las interacciones entre estos también fluctúen. Por ejemplo, se ha reportado (Goldberg y Novoplansky 1997) que la competencia suele ser débil al inicio de la época de lluvias, cuando el recurso está altamente disponible. Una vez que las plantas germinan, crecen o comienzan a ser fisiológicamente activas, la competencia se incrementa. Al término de la época de lluvias y mientras ocurre un periodo de sequía la competencia vuelve a disminuir. Los efectos competitivos ocurren principalmente cuando el recurso comienza a escasear, al término de la época de lluvias. Sin embargo, estos efectos también tienen consecuencias en los periodos de sequía, que pueden ser iniciados a diferentes tiempos debido a que las especies usan los recursos de manera diferencial o a que difieren en su fisiología o historias de vida.

Las especies pueden sortear las condiciones adversas través de distintos mecanismos de supervivencia o rasgos de historias de vida (Chesson y Huntly 1988), como por ejemplo volverse latentes (e.g. plantas geófitas), formar bancos de semillas (e.g. las especies anuales), almacenar y minimizar la pérdida de agua (e.g. plantas suculentas) e incluso a través de la presencia de raíces y rizomas los cuales almacenan energía y nutrientes obtenidos en años favorables (Coupland 1958). Una combinación simultánea de condiciones ambientales adversas y una competencia intensa podría ser fatal para la persistencia de las especies dentro de una comunidad. Sin embargo, estos rasgos de historia de vida pueden afectar el resultado de estas interacciones competitivas entre especies, amortiguando los efectos negativos de las interacciones bióticas y promoviendo el mantenimiento de la diversidad de especies a través del efecto de almacenamiento (Chesson y Huntly 1988).

La formación de bancos de semillas y la longevidad de los individuos podrían determinar si la variabilidad ambiental favorece o inhibe la persistencia de especies (Levine y Rees 2004). La gran variación en las tasas de germinación y en la longevidad de las semillas provocan que las especies de plantas difieran en su respuesta al medio ambiente, así como a las distintas interacciones que puedan darse entre planta-planta (Rees y Long 1992; Baskin y Baskin 2014) Por ejemplo, si durante los años adversos para una especie sus semillas se mantienen latentes, éstas no experimentarán los efectos de la competencia; lo contrario sucederá durante los años favorables, cuando las semillas germinan. La longevidad de los individuos también podría mitigar los efectos negativos de los ambientes con alta variabilidad temporal contribuyendo con la supervivencia de individuos en pie durante temporadas con bajas o nulas tasas de reclutamiento, para posteriormente contribuir el crecimiento poblacional reproduciéndose en épocas menos adversas (Harper *et al.* 1961; Chesson y Huntly 1988).

Efecto de las relaciones de parentesco y variabilidad ambiental sobre la coexistencia de especies

La diferenciación de nichos es fundamental para el mantenimiento de la diversidad mediante mecanismos de coexistencia estabilizadora (Adler *et al.* 2010). Por lo tanto, la cercanía evolutiva de las especies podría determinar la respuesta que éstas tienen frente a la variación ambiental, y por lo tanto la posibilidad de que los diferentes mecanismos de coexistencia operen. Al respecto, hay un cuerpo teórico amplio que enfatiza que las especies cercanamente emparentadas tienen nichos muy similares, por lo que la competencia entre ellas podría llegar a ser muy fuerte, resultando en la exclusión de una de ellas (Levine y HilleRisLambers 2009). Esto sugiere que la cercanía filogenética podría obstaculizar la coexistencia estable, pero favorecerse entre especies lejanamente emparentadas.

La pertenencia filogenética puede determinar las respuestas de las especies a las condiciones ambientales, en consecuencia, el tipo y la intensidad de las interacciones entre las mismas. Especies cercanamente emparentadas podrían tener respuestas semejantes a las condiciones ambientales que experimentan, contrario a las respuestas especie-específicas que requiere el efecto de almacenamiento para operar. Sin embargo, si la competencia entre las especies emparentadas es más intensa, tal como lo plantea la ecología de comunidades (Harper *et al.* 1961), entonces los efectos de la competencia serían más débiles bajo condiciones desfavorables. Esto se puede esperar debido a que los años adversos para una especie lo serían también para sus parientes, por lo que en dichos periodos habría pocos individuos de especies emparentadas interactuando. El papel del efecto de almacenamiento en la coexistencia de especies emparentadas dependerá de cuál de estos dos efectos opuestos sea más importante. Por otro lado, respuestas similares al ambiente conllevaría a mayores fluctuaciones en la demanda total de espacio. Esto se traduciría en mayores fluctuaciones en la intensidad de la competencia cuando las especies se encuentren más sincronizadas (más correlacionadas) en sus respuestas al ambiente (Yuan y Chesson 2015), promoviendo la coexistencia estable de especies a través de la no linealidad relativa.

Objetivos y preguntas de investigación

El mantenimiento de la diversidad implica la coexistencia de especies en comunidades ecológicas durante largos períodos de tiempo, y seguramente se debe a la acción de diversos mecanismos que operan simultáneamente y a diferentes escalas. Sin embargo, a pesar de los grandes avances teóricos en este campo, la evidencia empírica aún es escasa. Si bien hay mucha literatura disponible respecto al tema, la mayoría de los estudios se han enfocado en estudiar sólo un mecanismo de coexistencia a la vez y en comunidades poco diversas. Sólo algunos se han enfocado en determinar la fuerza de la estabilización, pero los mecanismos responsables de dicha estabilización rara vez se han determinado. Los efectos que la variabilidad ambiental tendrá sobre la diversidad de especies dependerán de su papel en la regulación en la coexistencia de especies.

Por lo anterior, es necesario un enfoque más cuantitativo, como lo plantea la teoría moderna de la coexistencia, para poder desagregar la importancia de los distintos mecanismos que promueven o limitan el mantenimiento de la diversidad. También nos permitiría entender cómo es que estos mecanismos se relacionan, qué factores determinan su intensidad o quizá desentrañar la manera en que operan.

La presente tesis tuvo como objetivo estudiar cómo las fluctuaciones temporales, las relaciones de parentesco entre las especies y la presencia de algunos atributos de historias de vida afectan la coexistencia de especies. Para ello, se determinó la contribución relativa de diferentes mecanismos a la coexistencia de 19 especies de pastos y herbáceas de un pastizal semiárido con alta diversidad. Además, se evalúa el papel de la cercanía evolutiva entre las especies y la presencia de bancos de semillas y la longevidad de individuos en pie sobre la magnitud de los mecanismos de coexistencia y sus componentes.

La investigación se desarrolló en un ecosistema en el que el agua parece ser el principal factor limitante. La precipitación anual es de 578 mm y es altamente variable (desviación estándar de 162 mm y un rango de 196-961 mm). Por lo que se esperaría que las especies respondieran a los cambios en la disponibilidad de este recurso. En esta comunidad vegetal se pueden encontrar hasta 25 especies de plantas vasculares en un área de 10 × 10 cm y la riqueza de especies asciende a más de 200 especies (Martorell *et al.* 2017), de ahí la importancia de estudiar los mecanismos que permiten el mantenimiento de su diversidad. La comunidad parece responder de manera diferencial a la variación interanual debido a que se observan cambios anuales en la composición. Las especies dominantes son pastos perenes (*Bouteloua* spp., *Microchloa kunthii*) y alrededor de la mitad de las especies en la comunidad son especies anuales. La mayoría de las especies perennes resisten las condiciones adversas gracias a los bancos de meristemos y las especies anuales dependen por completo de los bancos de semillas para su persistencia.

Debido a las características del sitio de estudio, la hipótesis del presente trabajo es que la variabilidad interanual y diferenciación de nichos permite la coexistencia de las especies debido a los mecanismos dependientes de las fluctuaciones, en particular del efecto de almacenamiento, los cuales dependen en parte de la dinámica del banco de semillas y de la longevidad de los individuos.

Objetivo general: Determinar el efecto de la variabilidad interanual, la distancia filogenética y ciertos atributos de historias de vida sobre la coexistencia de especies en un pastizal semiárido con alta diversidad.

Objetivos particulares:

1) Determinar si el efecto de almacenamiento explica la coexistencia de especies en un pastizal semiárido.
2) Caracterizar los bancos de semillas de las especies de estudio y evaluar su contribución al efecto de almacenamiento.
3) Evaluar la contribución de la longevidad de los individuos al efecto de almacenamiento.
4) Determinar el efecto de la filogenia sobre las condiciones causantes del efecto de almacenamiento y su impacto sobre la coexistencia de especies cercanamente emparentadas.

Estructura de la tesis

La tesis está formada por cinco secciones. La introducción y discusión general constituyen el marco conceptual del trabajo y sintetizan el alcance de la investigación. A continuación, se especifican los objetivos de investigación estudiados en el resto de los capítulos.

Capítulo I – *Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland*.

V. Zepeda y C. Martorell. 2019. Ecology. 100 (8), e02726

Hipótesis: El efecto de almacenamiento es el responsable del mantenimiento de la diversidad en el pastizal.

En este capítulo se determinó la contribución relativa de los diferentes mecanismos a la coexistencia de 19 especies de un pastizal semiárido. Se utilizó una serie de 13 años de datos de abundancia para calcular las tasas de crecimiento poblacional y coeficientes de competencia de cada especie de estudio. Después se realizaron análisis de invasibilidad para calcular la tasa de crecimiento poblacional a largo plazo y determinar la importancia de cada mecanismo de coexistencia y se evaluó cuantitativamente cada una de las condiciones que subyacen al efecto de almacenamiento.

Capítulo II – *Phylogenetic relatedness determines the strength of stable coexistence mechanisms in multispecies communities*.

V. Zepeda y C. Martorell. 2021. The American Naturalist. En prensa.

Hipótesis: Las relaciones de parentesco entre las especies afectan la intensidad de los mecanismos de coexistencia y su estabilidad.

En este capítulo se proponen nuevas hipótesis de cómo las relaciones de parentesco entre las especies pueden afectar los mecanismos de coexistencia dependientes e independientes de las fluctuaciones. Para ello, se utilizaron los datos obtenidos en el capítulo I, las tasas de crecimiento poblacional y coeficientes de competencia de cada una de las 19 especies, y se realizaron nuevas simulaciones y análisis de invasibilidad para abordar las siguientes preguntas: ¿Las especies cercanamente emparentadas presentan las mismas respuestas a la variabilidad ambiental? ¿La competencia es más intensa entre especies cercanamente emparentadas? ¿La riqueza de especies y su parentesco determinan la magnitud de los diferentes mecanismos de coexistencia estable?

¿Las especies cercanamente emparentadas tienen respuestas similares a las fluctuaciones temporales? ¿Cuál es el efecto de la sincronía en los comportamientos demográficos de las especies sobre los mecanismos de coexistencia dependientes de las fluctuaciones?

Capítulo III – *Mean life expectancy, but not seed banks, contributes to competition buffering in a semiarid grassland.*

V. Zepeda, E. J. González y C. Martorell. En preparación.

Hipótesis: Los bancos de semillas y la longevidad de los individuos amortiguan los efectos de la competencia durante periodos adversos.

En este capítulo se caracterizaron los bancos de semillas de las 19 especies de estudio a través de un experimento de supervivencia de semillas, que permanecieron hasta 30 meses en el suelo, y el monitoreo de abundancia de especies en el banco de semillas durante tres años. También se estimó la esperanza de vida promedio de nueve especies perennes, la cual se calculó a partir de datos de supervivencia y crecimiento que se tomaron para alrededor de 140 individuos de cada especie durante cinco años. Estos datos se relacionaron con los valores del parámetro que cuantifica el amortiguamiento (parámetro *b,* obtenido en el capítulo I). De ser cierta la hipótesis planteada, se esperaría que hubiera una relación positiva entre el tamaño del banco de semillas, la supervivencia de las semillas en el suelo, la esperanza de vida promedio y el parámetro *b*.

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Capítulo I

Fluctuation-independent niche differentiation and relative non-linearity maintain diversity in a species-rich grassland

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Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland

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Abstract. Despite the advances in ecological theory, evidence for the relative importance of the different mechanisms that promote species coexistence is lacking. Some mechanisms depend on the presence of interannual fluctuations in the environment combined with interspecific differences in the responses to such fluctuations. Among coexistence mechanisms, niche differentiation and storage effects have received much attention, whereas relative non-linearity (RNL) has been thought to be an unlikely and weak mechanism for multi-species coexistence and remains untested in nature. We quantified the relative contribution of different mechanisms to the coexistence of 19 grassland species by using field-parameterized population models and invasion analysis. Our results showed that 17 out of 19 species had the potential to coexist stably. Species diversity was maintained by RNL and large fluctuation-independent niche differences, i.e., between-species differentiation that is unrelated to interannual variations in environmental factors. Moreover, RNL increased the fitness of species that were less favored by niche differentiation, contributing to their persistence in the community. Storage effect was negligible or destabilizing, making no contribution to stable coexistence. These results, altogether with recent theoretical developments and indirect evidence in published data, call for a reassessment of RNL as a relevant mechanism for multi-species coexistence in nature.

Key words: environmental variability; equalizing mechanisms; fluctuation-dependent coexistence; multispecies competition; species coexistence theory; stabilizing mechanisms; storage effect.

Introduction

Coexisting species that compete for the same set of resources challenge classic ecological theory, as the number of species in natural communities seems to exceed the limits imposed by competition (Kremer and Klausmeier 2013). However, advances in ecological theory during the last two decades have provided new insights on diversity maintenance. Modern coexistence theory recognizes two different classes of mechanisms for coexistence. Equalizing mechanisms make fitness differences between species small, slowing competitive exclusion and enabling longer periods of co-occurrence (Chesson 2000). Such mechanisms are unstable as nothing prevents extinctions (Chesson 2000, HilleRisLambers et al. 2012). In contrast, stabilizing mechanisms grant indefinite coexistence as population growth rates increase when species become rare, preventing competitive exclusion (Chesson 2000, Adler et al. 2006, HilleRisLambers et al. 2012). If equalizing mechanisms are weak because fitness differences are large, one of the interacting species is in disadvantage. Strong stabilizing mechanisms are required to overcome this disadvantage and stabilize coexistence (Chesson 2000).

Several mechanisms stabilize coexistence. Some are independent of temporal fluctuations. For instance, some components of niche differentiation, such as resource partitioning or frequency-dependent predation, make intraspecific density-dependence stronger than interspecific regulation (Chesson 1994, 2000). This is stabilizing because, if a species becomes rare, the main checks on its population growth rate weaken and its numbers can increase. Other mechanisms with stabilization components are known as fluctuation dependent because they are driven by environmental variability (Chesson 2000, Yuan and Chesson 2015). These are the storage effect (SE) and relative non-linearity (RNL; Yuan and Chesson 2015).

In the SE, competition is buffered in a way that negative effects during unfavorable years do not outweigh the profits earned in favorable ones (Chesson 2000, 2003). For SE to occur, three conditions must be satisfied. (1) Differential responses to the environment: the

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environmental fluctuations have different effects on each species, so some of them experience a favorable year while their competitors undergo an adverse period. This may happen for instance in annual plant species that thrive in different years (Pake and Venable 1996), or germinate in different periods of the year (Holt and Chesson 2014). For this reason, SE has been considered as a form of temporal niche differentiation (Chesson et al. 2001). (2) Covariance between environment and competition: established populations experience less competition in unfavorable than in favorable years. For example, species that are active during specific times may face strong intraspecific competition during the periods that are favorable for their development (Chesson et al. 2004). (3) Buffered population growth (subadditivity): the joint negative effect of adverse years and competition on the population growth rate is smaller than the sum of both effects separately. This may happen if species endure adverse periods by means of cysts, seed banks, or large, longevous adults (Pake and Venable 1996, Cáceres 1997, Adler et al. 2006). Because such individuals are not affected by competition, the effects of this interaction are much smaller (i.e., are buffered) than in favorable periods.

RNL requires that species differ in the convexity of the relationship between competition and population growth rates (Chesson 2000, Yuan and Chesson 2015). If the relationship is convex, the population growth rate averaged over time increases in the presence of fluctuations, while the opposite occurs for concave functions (Chesson et al. 2004). This may allow a species to avoid extinction by increasing its population growth in the presence of fluctuations. Nonlinearity also determines the way in which a species drives fluctuations in competition (Chesson et al. 2004). Species with concave competition–growth relationships may increase fluctuations, which favor species with convex relationships. The opposite also occurs, as species with convex relationships reduce variations in competition. Thus, in RNL, individual species drive fluctuations in directions that favor their competitors but not themselves, preventing competitive exclusion (Huisman and Weissing 1999, Chesson 2000, Yuan and Chesson 2015). Fluctuations can be endogenous, arising from species activity (e.g., when species affect a resource base), or exogenous, if the interacting species merely buffer or amplify the effects of environmental variability (Yuan and Chesson 2015). Empiricists have focused on SE, and there are essentially no tests for RNL in nature, let alone its importance relative to SE (Letten et al. 2018).

Studies of the maintenance of species diversity have traditionally examined individual coexistence mechanisms, such as resource partitioning, frequency-dependent enemy attack or SE (Chesson 2000, 2018, Snyder et al. 2005). However, in nature, multiple mechanisms of coexistence are likely to operate simultaneously. Quantitative measurements are required to assess the relative importance of each mechanism, how they relate to each other, and if they depend on species traits such as their life history. Furthermore, while the strength of stabilization has sometimes been measured, the mechanisms responsible for such stabilization have seldom been determined (Adler et al. 2007, 2010, Levine and HilleRisLambers 2009, Chu and Adler 2015).

Our aim was to determine the roles of different coexistence mechanisms in maintaining diversity in a species-rich semiarid grassland using data for 19 species. Because of the large interannual variations in climate and species abundances at the study site, we placed special emphasis in two fluctuation-dependent mechanisms: relative nonlinearity and storage effect. To do so, we fitted population growth models using 13 yr of field data, and used them to analyze coexistence via the criterion of mutual invasibility: if all the species in a community have positive growth rates when rare, then they can avoid extinction and coexist with the others (Turelli 1978, 1980). We then used simulations and Chesson's quadratic approximation (Chesson 1994) to quantify the contribution of the different mechanisms to species coexistence.

METHODS

Data were collected in a species-rich (over 200 species and up to 25 species/dm^2) grassland at Concepción Buenavista, Oaxaca, southern Mexico (mean annual temperature = 16.3°C, annual rainfall = 578 mm (Martorell et al. 2017). Because climate is semiarid, water is probably an important limiting factor, and varies strongly across years (standard deviation = 162 mm, range 196–961 mm). Species seem to respond differently to annual variation in climate, with different species dominating the grassland in different years. Most dominant species are long-lived perennial grasses (*Bouteloua* spp., *Microchloa kunthii*), but about one-half of the species in the community are annuals. Most perennial species endure harsh, dry periods by maintaining a bank of viable meristems in spite of losing most of their biomass. Annuals have no alternative but to rely on seed banks.

All our data come from 0.1 × 0.1 m squares because this is the scale over which interactions occur given the tiny size of the plants (Watkinson and Freckleton 2001, Martorell and Freckleton 2014). Given the intense human activity in the area, it is impossible to use conspicuous marks in the field that could be easily found and removed by passersby. This made it difficult to find our marks rapidly, making it prohibitive to search for large numbers of squares marked individually. Instead, we randomly placed eight 1 × 1 m quadrants in each of 25 0.5-ha sites (i.e., there were 200 quadrats in total). In each quadrat, we randomly selected 20 squares. This meant that we had a total of 4,000 sampling units, but we only had to look for 200 marks. No physical barriers were used to delimit quadrats, but instead quadrats were marked only with two nails in opposite corners; a 1 × 1 m wooden frame was placed only during measurement.

The mean distance between any quadrat and its nearest neighbor was 14.97 m.

Every year, toward the end of the rainy season (late September–early October) we recorded the number of individuals of every species in each square. The same squares were sampled every year. Vegetative propagation and horizontal growth are very rare at the study site, so individuals can be easily distinguished from each other, even in grasses. New individuals are incorporated into the population mostly via sexual reproduction. Two exceptions are *Bouteloua polymorpha* and *Bouteloua chondrosioides,* where horizontal growth makes it difficult to count individuals, so only presence–absence in each square was recorded. We used data for the 19 most common species in the grassland (Table 1). The squares were followed over 13 yr (12 annual transitions).

To determine the role of different mechanisms on species coexistence, for each species j we fitted a version of the Hassell model (Hassell 1975). This model has been found to describe plant population dynamics accurately (Freckleton and Watkinson 2002). We modified the exponent of the Hassel model to permit non-additivity. The model was

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1+\sum_{k}\alpha_{j,k}N_{t,k}\right)^{\exp(a_j+b_j\ln\lambda_{j,t})}} \qquad (1)$$

where $N_{j,t}$ is the abundance of species j at time t, $\lambda_{j,t}$, is the intrinsic growth rate at time t, $\alpha_{j,k}$ is a per capita coefficient determining the competitive effect of species k on species j, and b_j determines the change in the exponent a_j as a result of environmental fluctuations. In the Hassell model the exponent is a constant, ω, but here it is a function of λ, which is a measure of how favorable or adverse a year is, thus allowing the effects of competition to change yearly as required if there is subadditivity (Chesson 1994). A positive value of b_j would increase the competition in favorable years, allowing SE to mediate coexistence. Subadditivity may result from a variety of life-history traits such as seed banks in annual plants or long-lived adults in perennial organisms. We found that adult survival and seed banks affect the exponent of the Hassell model, so ω decreases as seeds or established plants become more longevous (Appendix S1). Models used to study the effects of fluctuations on coexistence usually assume that germination or longevity change from year to year, so a fluctuating ω would be expected. This makes Eq. 1 a good option to represent a wide variety of life histories despite the fact that it does not explicitly incorporate their underlying attributes (Appendix S1).

Table 1. Study species.

Code	Species	Family	Life cycle
sd	*Stenandrium dulce*	Acanthaceae	perennial
fp	*Florestina pedata*	Asteraceae	annual
tm	*Tagetes micrantha*	Asteraceae	annual
ta	*Thymophylla aurantiaca*	Asteraceae	annual
sp	*Sanvitalia procumbens*	Asteraceae	annual
se	*Stevia ephemera*	Asteraceae	annual
hp	*Heterosperma pinnatum*	Asteraceae	annual
tc	*Tridax coronopifolia*	Asteraceae	annual
cs	*Cyperus seslerioides*	Cyperaceae	perennial
bt	*Bulbostylis tenuifolia*	Cyperaceae	perennial
pn	*Plantago nivea*	Plantaginaceae	perennial
bp	*Bouteloua polymorpha*	Poaceae	perennial
bc	*Bouteloua chondrosioides*	Poaceae	perennial
st	*Sporobolus tenuissimus*	Poaceae	perennial
mk	*Microchloa kunthii*	Poaceae	perennial
mp	*Muhlenbergia peruviana*	Poaceae	annual
aa	*Aristida adscensionis*	Poaceae	annual
rt	*Richardia tricocca*	Rubiaceae	perennial
cd	*Crusea diversifolia*	Rubiaceae	annual

Note: Code indicates the abbreviation of species names used in the figures.

All the parameters in Eq. 1 were estimated by maximizing the likelihood of a non-linear regression of the observed $N_{j,t+1}$ on $N_{j,t}$. We included the effect of the environmental fluctuations in the model by estimating different, $\lambda_{j,t}$, for each year t. The per-capita intensity $\alpha_{j,k}$ of intra and interspecific competitive interactions, as well as a_j and b_j were assumed to be constant over time. If individuals are larger or smaller in different years, we could expect alphas to vary because the effects of competition frequently depend on plant size (Weiner 1990). However, this is not the case at our study site (Appendix S2). Also, it can be shown that our results were consistent with a scenario with constant alphas (Appendix S2). Because plants are tiny, we are assuming that any plant interacts only with individuals that grow in its own square (Watkinson and Freckleton 2001, Martorell and Freckleton 2014). Therefore, for fitting purposes, population sizes $N_{t,k}$ of all species were those recorded in the same square as $N_{j,t}$ and $N_{j,t+1}$. Movement of individuals (seeds) between squares may bias the estimates of intraspecific interactions (Freckleton and Watkinson 2001). Thus, during model fitting, we considered that a fraction of the seeds move between squares. Based on preliminary results, we decided to model dispersal by allocating the same number of immigrant seeds to all squares in a quadrat (Appendix S3). This number was allowed to vary between years and squares. Because of poor model identifiability, we penalized the likelihood so the values of a_j and b_j were restricted in a way that resulted in ω values near one, as has been observed in many studies on plant population dynamics (Freckleton and Watkinson 2002).We considered all squares to be independent of each other, as data suggest that membership to different quadrats has a relatively small effect on population dynamics (Appendix S4).

We used invasion analysis to determine coexistence. Invasion analysis is based on the long term, low density population growth rate $\overline{r_i} = \ln\left(N_{i,t+1}/N_{i,t}\right)$ of an invader species i (i.e., a species that is nearly absent of the community, such that its density is effectively zero) in the presence of its competitors, which are allowed to approach their stationary state and are termed residents (Chesson 2000). It is important to note that a positive value of $\bar{r}_i$ means that species i can invade the system. If all species have positive $\bar{r}_i$ values, then none will go extinct and stable coexistence is possible. The $\bar{r}_i$ can be partitioned into the contributions of different mechanisms to coexistence using Chesson's (1994) quadratic approximation. To use this method, Eq. 1 needs to be rewritten in a standard form. To do so, we defined $E_{j,t} = \ln(\lambda_{j,t})$ and $C_{j,t} = \ln(1 + \Sigma\alpha_{j,k}N_{t,k})$. With these definitions, $C_{j,t}$ reflects competition and the term $E_{j,t}$ is directly related to fitness and thus to equalizing mechanisms. $E_{j,t}$ also reflects directly the effects of environmental fluctuations on species performance. Therefore, the growth rate can be rewritten as

$$r_{j,t} = E_{j,t} - e^{a_j + b_j \ln\lambda_{j,t}} C_{jt}. \tag{2}$$

Instead of $E_{j,t}$ and $C_{j,t}$, it is handy to use $\mathcal{E}_{j,t}$ and $\mathcal{C}_{j,t}$, which are standardized (Appendix S5). This simplifies the expansion of Eq. 1 by means of Taylor series. The standardization requires a somewhat arbitrary reference value, which we chose to be equal to the mean of the $E_{j,t}$ values for each species. This makes the mean of the $\mathcal{E}_{j,t}$ of each species over time very close to zero, and results in a quite accurate quadratic approximation. After standardization and Taylor expansion, Eq. 2 can be rewritten as

$$r_{j,t} = \mathcal{E}_{j,t} - \mathcal{C}_{j,t} + \gamma_j \mathcal{E}_{j,t} \mathcal{C}_{j,t} \tag{3}$$

where and $\gamma_j = b_j / \left(b_j \overline{\ln\lambda_{j,t}} - 1\right)$ (Appendix S5). This last parameter is a measure of non-additivity, which is crucial for the storage effect. The interaction between environment and competition is subadditive only if $\gamma_j < 0$, which only occurs if $0 < b < 1/\overline{\ln\lambda_{j,t}}$. Following Chesson's framework, from Eq. 3, we can obtain

$$\bar{r}_i = r_i' - \Delta N_i + \Delta I_i = (\Delta\mathcal{E}_i - \mathcal{C}_i^{\{-i\}^*}) - \Delta N_i + \Delta I_i \tag{4}$$

where r_i' is the contribution of fluctuation-independent mechanisms to $\bar{r}_i$, ΔN and ΔI are the contributions of RNL and SE, respectively, $\Delta\mathcal{E}$ is the mean environment effect on $\bar{r}_i$ and reflects the fitness differences, and $\mathcal{C}^{\{-i\}^*}$ reflects the fluctuation-independent difference between interspecific and intraspecific competition (Chesson 1994, 2000). Small $\Delta\mathcal{E}$ values contribute to equalization. Negative $\mathcal{C}^{\{-i\}^*}$ values indicate stronger intra than interspecific regulation and thus act as a stabilizing mechanism (Chesson 2000). It must be noted that negative values of $\mathcal{C}^{\{-i\}^*}$ and ΔN contribute positively to $\bar{r}_i$, so, for ease of interpretation, we will always report them after changing their signs. $\Delta\mathcal{E}$, $\mathcal{C}^{\{-i\}^*}$, ΔN, and ΔI were calculated using the estimated parameters for Eq. 1. See Appendix S5 for details.

The accuracy of $\bar{r}_i$, ΔI and ΔN estimates may be compromised if the quadratic approximation's assumptions are not met, but alternative estimates can be obtained directly from Eq. 1 without resorting to those assumptions. To do so, we ran simulations in which we estimated changes in the densities of each species over time by iterating Eq. 1. To include environmental fluctuations, in each iteration, we selected randomly and with equal probabilities one out of the 12 annual transitions that we observed. The $\lambda_{j,t}$ values for that transition were used in the projection of population sizes into the next year. To conduct invasibility analysis, we set the density of one species (the invader) to zero, the densities for the residents to 0.1. The model was iterated for 4 million times. The first 2 million iterations were dropped to remove transients and allow the residents to reach their stationary densities. The growth rate r_i of the invader was estimated from the remaining 2 million iterations. The r_i values were averaged over to obtain $\bar{r}_i$. We conducted three sets of simulations. In the first one we used the observed parameters and obtained $\bar{r}_{i,\mathrm{obs}}$. In the second one, we set $b_i = 0$ for the invader and calculated $\bar{r}_{i,b=0}$. This has the effect of making the model additive and thus eliminates the storage effect. In the third set, the λ values of all the species were set to their respective geometric means, making the environment constant, and obtained $\bar{r}_{i,\mathrm{const}}$. This procedure removes any exogenous fluctuation in the system, and thus eliminates both the storage effect and (in the absence of endogenous fluctuations) the relative non-linearity. We then estimated $\Delta\hat{I} = \bar{r}_{i,\mathrm{obs}} - \bar{r}_{i,b=0}$, and $\Delta\hat{N} = \bar{r}_{i,\mathrm{const}} - \bar{r}_{i,b=0}$.

We assess which of the ingredients of the SE, if any, may contribute to coexistence. Differences in responses to the environment were assessed by correlating λ for each pair of species over time. λ values are a bioassay of the responses of each species to the interannual variability, so a correlation near one means that species have similar responses. Environment–competition covariances were calculated from the time series of $\mathcal{E}$ and $\mathcal{C}$ obtained during the quadratic approximation calculations. Finally, subadditivity was measured as γ_j.

RESULTS

The results of the fitting procedure (parameter estimates and standard errors) as well as $\Delta\mathcal{E}$, $\Delta\mathcal{C}$, ΔN, ΔI values and environment–competition covariances are reported in Appendix S6.

Interannual environmental fluctuations had strong effects on the intrinsic population growth rates λ of the studied species (mean CV of ln λ of all species = 0.843). However, not all species were equally sensitive to the fluctuations (smallest CV = 0.128, largest CV = 5.158). The variance in λ values was larger for annuals than for perennials (Mann-Whitney U test $P = 0.035$). Intraspecific competition coefficients were much larger than interspecific ones (Fig. 1).

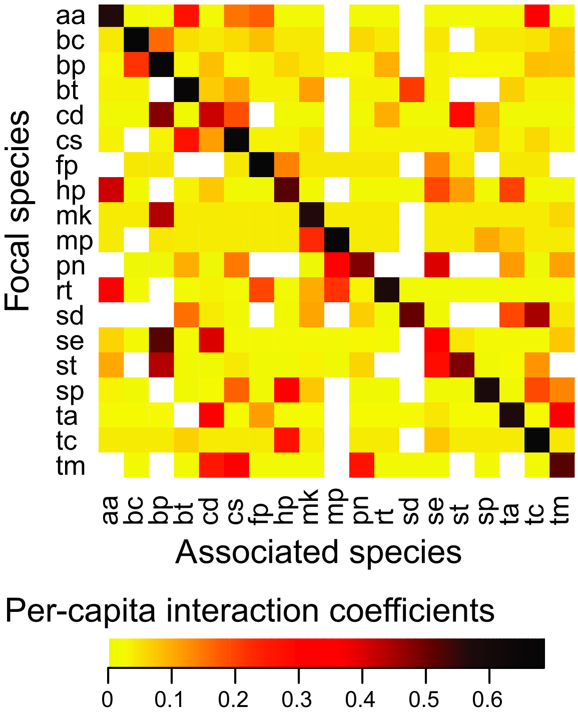

FIG. 1. Per-capita interaction coefficients α for species pairs. White tiles correspond to coefficients that could not be estimated due to insufficient data. See Table 1 for species names.

The invasion analysis showed that 17 out of the 19 species had the potential to coexist stably with the others in the community as they had positive values of long-term, low-density, growth rates ($\bar{r}_i$; Fig. 2). We found strong evidence that coexistence in this grassland is stabilized by fluctuation-independent mechanisms followed by relative non-linearity (RNL) because $\mathcal{C}^{\{-i\}^*}$ and ΔN made the strongest positive contributions to $\bar{r}_i$ (Fig. 2). ΔN was positive in about one-third of the species (e.g., *Aristida adscensionis* and *Stevia ephemera*), and negative in about another one-third (e.g., *Heterosperma pinnatum* and *Thymophylla aurantiaca*). The remaining species were essentially unaffected by RNL (Fig. 2). These results were similar regardless of whether simulations or the quadratic approximation were used to partition mechanisms (correlation between values from both methods were $r = 0.99$ for $\bar{r}_i$, and $r = 0.84$ for RNL). Most $\Delta \mathcal{E}$ values were small (Fig. 2) indicating that equalization was important given our standardization procedure (Appendix S5).

The magnitudes of the storage effect (SE) were very different depending on the method used to estimate it (Fig. 2; Appendix 6: Table 3). In the quadratic approximation, most ΔI values were close to zero, indicating that the influence of SE on coexistence was negligible (Fig. 2). In contrast, $\Delta \hat{I}$ was large and negative in a few species, which were the same for which the quadratic approximation found negative $\Delta \mathcal{E}$ values. In fact, $\Delta \hat{I}$ and $\Delta \mathcal{E}$ were strongly correlated ($r = 0.96$, $P < 0.001$) and had similar magnitudes. Negative $\Delta \hat{I}$ would indicate that the SE destabilizes coexistence. Regarding the ingredients of the SE, most of the correlations between λ values were positive (although only a few were strong) suggesting that a favorable year for a species was also a favorable year for its competitors (Fig. 3a). Environment–competition covariances for each species were in general very close to zero in the quadratic approximation (absolute value of the covariance averaged over all species as residents was 5.28×10^{-5}, maximum 3.34×10^{-4}, and as invaders the average was 2.23×10^{-5}, maximum 1.24×10^{-4}), but in the simulations, these covariances were substantially larger (on average over 50 times larger for residents, and five orders of magnitude larger for invaders) although still small for most species (Fig. 3b). Note that in some species, environment-competition covariance as invaders was positive (Fig 3b.). These species had negative $\Delta \hat{I}$ values. Subadditivity was close to zero in 58% of the species, precluding SE to promote coexistence (Fig. 3c).

Finally, we analyzed if the contributions of the different coexistence mechanisms were correlated (Spearman rank correlation) and if they differed between species with different life cycles (Mann-Whitney U test). Only $\mathcal{C}^{\{-i\}^*}$ and ΔN were correlated ($\rho = -0.57$, $P = 0.010$). We found no significant differences between annuals and perennials.

We tested the robustness of our results to certain assumptions of the fitting procedure (Appendix S4). The use of time series to fit models of population dynamics is based on the idea that variations in natural densities reproduce a response surface design (Golberg and Scheiner 1993). This requires that species co-occur frequently enough, and in enough combinations of density. Squares with high abundances of more than one species are rare in our data. Nevertheless, simulations show that this had no effect on the accuracy of the estimates (Appendix S4). Another problem with the time-series approach is that seeds produced many years in the past may germinate at any moment, obscuring the relationship between N_t and N_{t+1}. About one-half of our species lack seed banks, and most of the remaining species have short-lived seeds (Appendix S4). This suggests that seed banks are not a generalized problem. We also analyzed whether measurement error could bias some of our parameters, finding that it would not affect the relative importance of coexistence mechanisms (Appendix S4).

DISCUSSION

Our study provides empirical evidence regarding key questions about diversity maintenance: first, fluctuation-independent stabilizing mechanisms promote species coexistence prominently (Fig. 2), and second, relative nonlinearity (RNL) plays an important role in

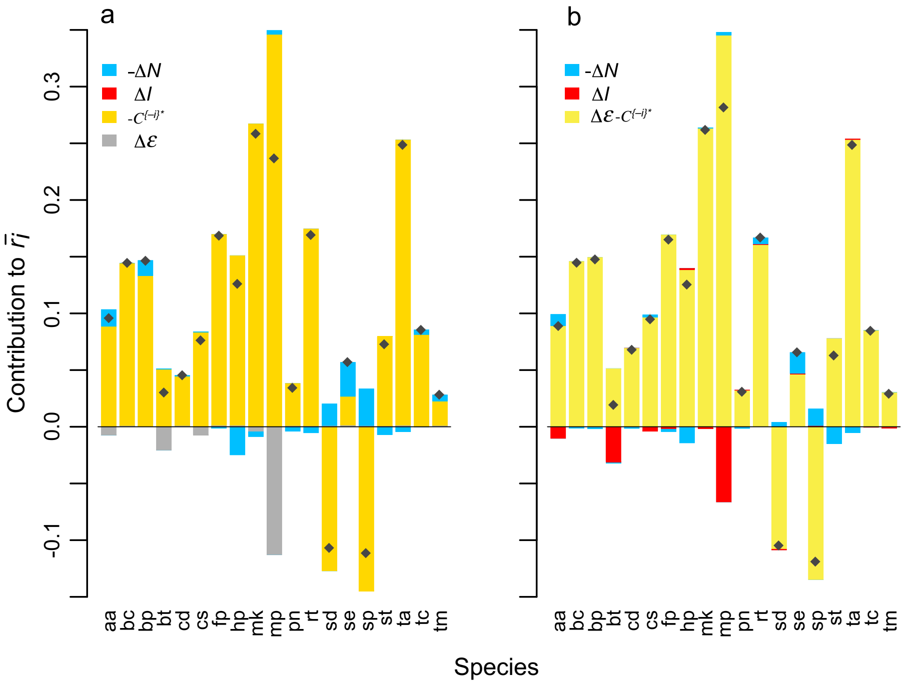

FIG. 2. Contributions of different coexistence mechanisms to the low-density, long-term, population growth rate, $\bar{r}_i$,estimated using (a) the quadratic approximation or (b) the simulations. $\Delta\mathcal{E}$ indicates fitness differences, which, if small, promote strong equalization. $\mathcal{C}^{\{-i\}^*}$ is the fluctuation-independent niche differentiation. ΔN and ΔI are the contributions of relative non-linearity and the storage effect, respectively. Black diamonds are the $\bar{r}_i$ for each study species. Species with negative $\bar{r}_i$ values are not able to persist in the community. See Table 1 for species names. The signs of $\mathcal{C}^{\{-i\}^*}$ and ΔN have been changed for clarity, so positive values make positive contributions to $\bar{r}_i$.

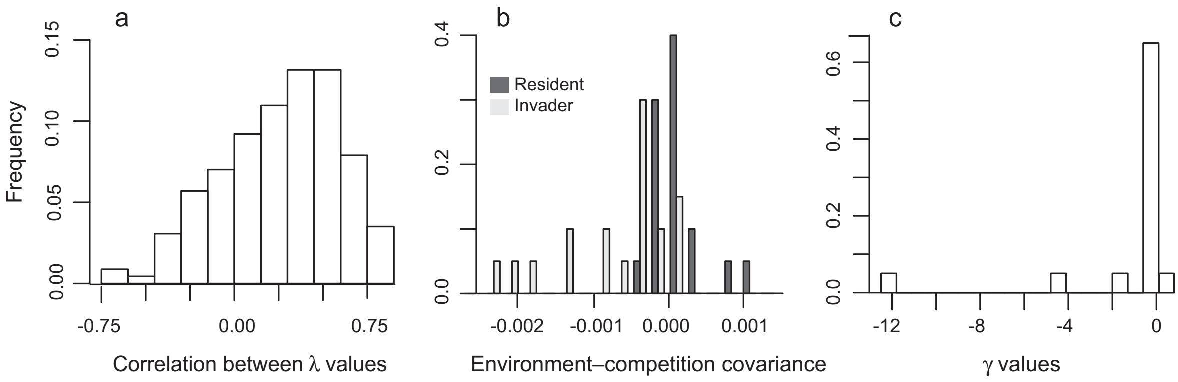

FIG. 3. Indicators of the conditions that give rise to the storage effect: (a) differential responses to the environment, measured as the correlations between the annual intrinsic population growth rates (λ) of every pair of species; (b) covariance between environment and competition experienced by each species as an invader and as a resident; (c) buffered population growth, measured as γ_j values (two extreme values are not shown).

multispecies coexistence, whereas the storage effect (SE) seems to be irrelevant or may even hinder coexistence (Fig. 2).

Temporal fluctuation independent mechanisms

Small $\Delta\mathcal{E}$ values would indicate that fitness differences are minimal, and thus that equalizing mechanisms play a significant role in coexistence (Fig. 2). This would be in line with many studies that have found very small $\Delta\mathcal{E}$ values (Adler et al. 2007, 2010, Chu and Adler 2015). However, the partition of r_i' into $\Delta\mathcal{E}$ and $\mathcal{C}^{\{-i\}^*}$ depends on the reference values used to standardize the model (Chesson 1994). Because we standardized with respect to the mean population growth rate for each species, mean E values must be close to zero and $\Delta\mathcal{E}$ can only be small (see Fluctuation-dependent mechanisms section for the exceptions to this rule in Fig. 2). However the sum (r_i') of $\Delta\mathcal{E}$ and

$\mathcal{C}^{\{-i\}^*}$ is the same regardless of the parameterization (Chesson 1994), making them dependent on each other. Thus, given our standardization and considering that coexistence only occurs if stabilization is strong enough to counter any fitness disadvantages, $\mathcal{C}^{\{-i\}^*}$ may be interpreted as how much stronger stabilizing mechanisms are compared to the minimum strength required for coexistence. $\mathcal{C}^{\{-i\}^*}$ would then be a measure of the so-called "embarrassment of niches" (Adler et al. 2010).

The strong stabilizing forces observed (large $\mathcal{C}^{\{-i\}^*}$ values; Fig. 2) were the result of greater intraspecific compared to interspecific competition (Fig. 1; Chesson 2000). A common problem when fitting time series is that, if there is measurement error, intraspecific competition tends to be overestimated (Freckleton et al. 2006). This raises the question of whether our large $\mathcal{C}^{\{-i\}^*}$ are an artifact. We analyzed the possible effect of measurement error on parameter estimation (Appendix S4). Some small errors and biases may be introduced, but the error in the estimates of interspecific competition would be similar to the error in intraspecific interactions, so the pattern that intraspecific alphas are larger than interspecific ones is not an artifact (Appendix S4).

Another issue is that we used observational data, which results in larger estimations of the ratio of intra to interspecific interactions than experimental studies (Adler et al. 2018). If this is an artifact, it would mean that, in studies such as ours, $\mathcal{C}^{\{-i\}^*}$ would tend to be overestimated. Alternatively, the bias may occur not in observational studies but in experiments if they are short term, precluding plant-soil feedbacks from developing (Adler et al. 2018), or if they take place under controlled conditions where the environment is simplified eliminating some axes over which niches may be different. On the other hand, α-values estimated from observations reflect not only competition, but also other processes. The consideration of the net effects that species have on each other, plus the factors that modify such effects, is probably an asset: coexistence mechanisms arise from a multitude of concurrent processes, not only competition (Chesson 2000).

Greater intra than interspecific competition is the signature of niche differentiation (Levine and HilleRisLambers 2009). Because ΔI and ΔN encompass the temporal dimensions of the niche, $\mathcal{C}^{\{-i\}^*}$ considers only fluctuation-independent niche differentiation (FIND). Our $\mathcal{C}^{\{-i\}^*}$ estimates are likely to arise from specialist predators, as happens in various communities throughout the world (Petermann et al. 2008, Comita et al. 2010, Johnson et al. 2012), and from forms of resource differentiation not related to interannual fluctuations. On the other hand, there may be other factors that affect $\mathcal{C}^{\{-i\}^*}$ in our system but that could not be captured by our model, such as spatial heterogeneity in water availability (Martorell et al. 2015). In fact, one of the species that cannot coexist stably with the others according to our results occurs only in very deep and humid soils (*Stenandrium dulce*) where the other study species are not very common. We believe that in a model that accounts for spatial variations in water availability, coexistence would be possible because *S. dulce* would find areas were its competitors are scarce.

Fluctuation-dependent mechanisms

As in previous studies (Adler et al. 2009, 2010, Chu and Adler 2015), the removal of temporal fluctuations did not greatly affect the long-term, low-density population growth rate $\bar{r}_i$, indicating that interannual variation plays a secondary role in species coexistence at our system (Fig. 2). However, the results obtained by this procedure only reflect the effects of environmental fluctuations on diversity maintenance, but do not reveal the underlying mechanism: SE or RNL. Moreover, differences between simulations with and without environmental variability do not necessarily reflect fluctuation-dependent mechanisms, because they do not necessarily result from exogenous environmental fluctuations. For instance, resource consumption causes chaotic fluctuations in species abundances that allow the coexistence by RNL of large numbers of species even in the absence of external variability (Armstrong and McGehee 1980, Huisman and Weissing 1999). Direct measurements of the contributions of SE and RNL are necessary to solve these issues.

There was a disagreement in the contributions of SE to coexistence between the quadratic approximation and the simulations. This was probably the result of the approximation's inability to reproduce the environment-competition covariances properly. In the original model, these covariances were substantially larger than in the approximation, where they were very close to zero (Appendix S6). Consequently, the SE could not be but negligible. The problem with the approximation probably arose in part because of large fluctuations in λ (violating one of the assumptions of Chesson's framework), but mainly from inaccurate estimates provided by the quadratic Taylor expansion, i.e., cubic or higher-order terms are seemingly important for the approximation especially for those species that may have SE because $b > 0$ (Appendix S5). Under such circumstances, the effect of SE on $\bar{r}_i$ would be assigned to the effect of the environment, $\Delta\mathcal{E}$, and not to the joint effect of competition and environment, ΔI. Moreover, if the $\Delta\mathcal{E}$ values in the quadratic approximation are in fact ΔI, the real values of $\Delta\mathcal{E}$ should be very close to zero as required given our standardization choices.

Storage effect was not relevant for stabilizing coexistence in any species. It was either small or made negative contributions to $\bar{r}_i$. Small effects of the SE have been reported frequently (Adler et al. 2010, Chu and Adler 2015, Ellner et al. 2016). In our study, this is the result of all three ingredients of the SE. Buffered population growth was absent (γ_j was nearly zero; Fig. 3c) in about half of the species. Species-specific responses to the environment were confirmed, but differences between species were relatively small (the majority of the correlations of annual growth rates between species were > 0.5; Fig. 3a). This was probably the result of most species thriving on rainy years and declining during drought (CM, *personal observation*). Finally, environment–competition covariances were very small (Fig. 3b). This could potentially be the result of how we specified the equations for population growth, where competition coefficients α are assumed to remain constant over time (Appendix S3). However, extensive simulations show that in systems with fluctuating α values, large b values should be estimated (Appendix S2). The fact that our b values were small implies that α is more or less constant over time, and thus that our formulation of the model is appropriate (See Appendix S2 for further details). The magnitude of the SE may also depend on the interannual autocorrelation in environmental conditions (Levine and Rees 2004), which was not included in our model. However, we found no evidence for such phenomenon in our data (Appendix S7).

Strongly negative SE as the ones that we observed for four species has rarely been reported (but see Li 2015). Species with negative $\Delta\hat{I}$ values had large, positive environment–competition covariances as invaders (Fig. 3b). As a result, environmentally benign years are also competitively challenging. Thus, the invader's invasion rate was impaired compared with species with small or even negative covariances because it cannot profit as much from favorable periods. Positive invader environment–competition covariances may arise if the responses of the different species to the environment are correlated, as in our study. This has been found to result in negative SE (Li 2015, Yuan and Chesson 2015). Moreover, most of the environment-competition covariances for species as residents were negative, contrary to what is required for the SE to be positive.

Our results indicate that RNL may be far more important for promoting coexistence than SE, although secondary to FIND (Fig. 2). The relatively high correlation between $\Delta\hat{N}$ and ΔN suggests that RNL (which was calculated by removing the exogenous temporal variability and removing the contribution of SE) is the result of exogenous fluctuations. Moreover, in our simulations without environmental variability, we observed that population sizes remained constant over time, ruling out the possibility that ΔN arises from endogenous fluctuations. Because RNL refers to nonlinear relationships between the population growth rate and competition, it would seem that RNL results from changes in the population sizes of competitors driven by interannual variability (Yuan and Chesson 2015).

Based on recent theoretical advances, it seems that fluctuations in recruitment underlie RNL in our study system. Recruitment is the sole driver of competition and is the only factor that responds to environmental fluctuations in the lottery model. In that model, RNL can be much more important than SE when (1) more than two species are considered, (2) there is variation in the species longevities, and (3) short-lived species are more sensitive to environmental fluctuations than long-lived ones (Yuan and Chesson 2015). Our system complies with all three conditions: recruitment is an important driver of population dynamics, varies strongly across years, and seedlings are more sensitive to competition than adults (Martorell and Freckleton 2014). Our results that annuals suffer greater annual variations in λ than perennials are also in line with the third condition listed above (although we are not considering seed bank longevity). Thus, the main drivers in the lottery model could also be relevant at our grassland.

The question arises of how common and strong is RNL in the natural world. While much uncertainty remains, we would argue that it probably is. First, fluctuations occur widely in nature. RNL may arise from the internal dynamics of the system, especially when there are several species and resources (Armstrong and McGehee 1980, Huisman and Weissing 1999, Yuan and Chesson 2015), or from fluctuations in competition due to climatic-driven changes in population densities. Second, species differ in their sensitivity to environmental fluctuations. This means that, in certain resident-invader scenarios, fluctuations in competition may be larger than in others, which is a necessary condition for RNL to occur (Yuan and Chesson 2015). The fact that in our study, variability in λ differs strongly between species seems to illustrate this situation. Third, many communities seem to be driven by limitations during recruitment (competition, natural enemies), a condition that seems to promote RNL (Yuan and Chesson 2015). Fourth, some studies have found that fluctuations promote coexistence (Levine and Rees 2004, Descamps-Julien and González 2005, Adler et al. 2006, 2009, 2010, Chu and Adler 2015), a result that has usually been attributed to the SE. However, recent reanalyses suggest strongly that in fact coexistence may be the result of RNL (Ellner et al. 2016). The only study in which RNL and SE have been measured in an empirical system supports the notion that SE is less important for coexistence than RNL (Letten et al. 2018).

Unlike SE and FIND, positive effects of RNL in some species necessarily imply negative effects on others (Chesson 1994). Thus, RNL can promote coexistence, but also limit it. This was not the case in our study, where FIND and RNL were negatively correlated so the species that suffered negative effects of RNL were those where FIND promoted coexistence more strongly. In contrast, RNL favored the species that tended to be in greater risk of extinction, i.e., those in which FIND did not strongly stabilize coexistence. (Fig. 2). This correlation may be the result of intrinsic attributes of plant life-histories, or else from the exclusion during community assembly of species with negative invasion rates due to small FIND and negative RNL.

In our study site, FIND seems to be a main driver of stabilization, followed by RNL. As in many other studies, SE was not so important and was even destabilizing for a few species. We need a deeper understanding of the conditions that make RNL important in nature and why it may evolve or be maintained despite the evolutionary forces that seem to undermine it (Hartig et al. 2014). It is important to re-examine previous results to assess the roles of SE and RNL more directly with appropriate theory, data and rigorous quantitative analysis. Finally, the fact that temporal fluctuations have small effects on coexistence in many systems highlights the need for a more detailed understanding of FIND and its drivers.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2726/suppinfo

DATA AVAILABILITY

Codes for simulation, data extraction, and analyses are available on GitHub

Supporting Information. Zepeda, V., and C. Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*.

Appendix S1. Relationship between the model used in this study and mechanistic models with storage effects

It is thought that the storage effect can arise in life cycles that are characterized by the presence of stages that can endure adverse conditions and last for several years (Chesson 2000). Thus, the models that are used to study the storage effect usually contain such stages explicitly, such as seed banks or perennial individuals (Pake and Venable 1995, 1996, Cáceres 1997, Adondakis and Venable 2004, Adler et al. 2006). In our study we include species that differ widely in their life cycle and may have more than one of such stages. Given the difficulties already involved in the parameter estimation when many species are present, and the complexity and variation in their life histories, it proved impossible to study a complex model that represented the population dynamics in a mechanistic way. Thus, we used a "generic" model that had the minimal characteristics required to study the storage effect, namely environmental and competitive effects and non-additivity:

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1+\sum_{l=1}^{s}\alpha_{jl}N_l\right)^{\omega_j}} \qquad \text{(Eq. S1)}$$

where $N_{j,t}$ is the number of individuals in the population at time t, $\lambda_{j,t}$, is the intrinsic growth rate (*i.e.*, in the absence of competition) of the population at time t, α_{jl} is the per-capita competition effect of species l on species j, $\omega_j = \exp(a + b \ln\lambda_{j,t})$ and s is the number of species in the community.

The question arises if this model represents appropriately the underlying mechanisms that may cause the storage effect, and how it relates to models in which the storage effect has been studied. In particular, we chose to modify ω_j in the Hassell model to include non-additivity in the model, which is precisely the attribute of the population dynamics that arises from the presence of long-lived stages in the life cycle.

To show that ω_j reflects the presence of seed banks or perennial individuals, we used mechanistic models to generate time series of abundances that resembled our field data, and obtained the respective ω_j values. We detail the procedure in what follows (see also the code at the end of this appendix):

Step 1: Selection of mechanistic models. We used two models for a single species. The first one had seed banks (Chesson 1994):

$$S_{t+1} = \sigma(1-g)S_t + \frac{g\varphi}{1+\alpha g S_t}S_t \qquad \text{(Eq. S2)}$$

where S_t is the number of seeds at time t, σ is the survival probability of the seeds in the bank, g is the germination probability, φ is the number of seeds produced on average per seed that germinates, and α is a competition coefficient. Note that the second term in the sum has the same form as the Hassell model for a single species with $\omega = 1$. The second model includes perennial individuals:

$$N_{t+1} = \sigma N_t + \frac{\varphi}{1+\alpha N_t} N_t \quad \text{(Eq. S3)}$$

where N_t is the number of established plants at time t, σ is the survival probability of those plants, φ is the number of new established plants produced on average per established plant, and α is a competition coefficient. Note the same relationship with the Hassell model as in Eq. S2.

Step 2: Time-series simulation: In all cases we simulated eleven years of data (ten annual transitions) for 1 000 "quadrats" to make the dataset analogous to our field data. Each "quadrat" was initialized by assigning a random number of seeds or plants to it. This number came from a uniform distribution with limits at 0 and 20. For the model with a seed bank, we recorded the number of established individuals in each year and quadrat, $N_t = gS_t$, which corresponds to the actual figure that we recorded in the field. In the model with perennial individuals we obtained N_t directly from Eq. S3. Thus, we had 10 000 data in each time series.

Step 3: Estimation of ω: For each time series we fitted Eq. S1 by maximum likelihood using the package bbmle (Bolker and Team 2002) and assuming normal error. This was done in two steps: first we applied simulated annealing to explore the parameter space (option method = "SANN" in bbmle) and obtain an approximate set of values for α, λ, and ω. To obtain more precise estimates, we used the approximate figures as starting values of a second round of optimization using the Nelder-Mead algorithm (the default in bbmle). As in our analysis of real data we constrained α, λ, and ω to have positive values by means of exponentiation.

Step 4: Relating seed banks and perenniality to ω_j: Eqns. S2 and S3 reduce to a simple Hassell model with $\omega_j = 1$ if long-lived stages are absent in the life cycle. If ω_j reflects the presence of long-lived stages, it should deviate monotonically from 1 as the seed bank or the established plants become more longevous. This occurs as σ is increased and as g diminishes. Thus, we ran three sets of simulations. In the seed bank model, we produced ten time series, each with $g = \{0.1, 0.2, \ldots, 1\}$. This was repeated using $\sigma = 0.5$ and $\sigma = 0.75$. The remaining parameters were fixed at $\varphi = 5$ and $\alpha = 0.5$. Note that if $g = 1$, no seed bank is present. For the model with perennial individuals, ten simulations were produced with $\sigma = \{0, 0.1, \ldots, 0.9\}$. The remaining parameters were fixed at $\varphi = 2$ and $\alpha = 0.5$ (other choices of φ and α do not seem to affect the relevant results in either model). In this model, no perennial individuals persist if $\sigma = 0$.

For each of the 30 time series we estimated ω_j as detailed in Step 3. Regardless of the model, the estimated value of ω_j was very close to one under the conditions where there was no persistent stage in the population, but ω_j became smaller as the seed bank or the established plants became more longevous (Fig. S1).

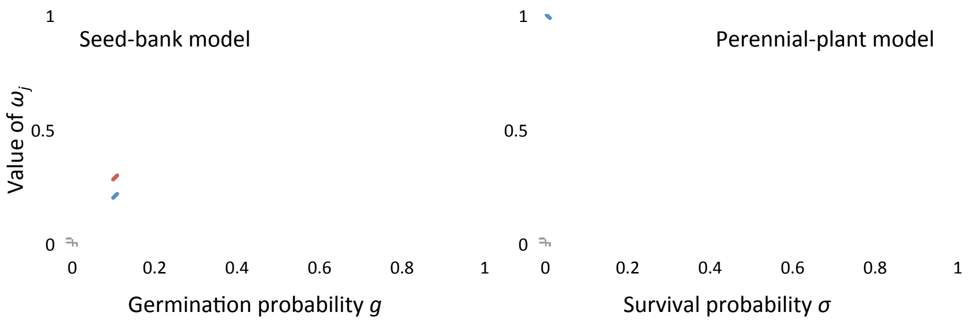

Fig. S1. Estimated ω_j values depending on the longevity of the seed bank (left) or of the established plants (right). In the seed-bank model, the red line corresponds to a seed survival probability of 0.5, and the blue line to a probability of 0.75.

Thus, we consider that the value of ω_j is an excellent candidate to reflect the presence of seed banks and perennial individuals. If survival or germination fluctuate over time, this is likely to affect ω_j, and thus we decided to make it a function of the environmentally dependent parameter $E_{j,t} = \ln\lambda_{j,t}$ by setting $\omega_j = e^{a_j + b_j \ln\lambda_{j,t}}$ (Appendix S5). This affects non-additivity, as it is to be expected. For instance, in the seed bank model, the parameter that determines non-additivity $\gamma = 1 - (1-\sigma)^{-1}$ (Chesson 1994). Because of the close relationship between g, σ and ω, γ should also be related to ω. In fact,

$$\gamma_j = \frac{b_j}{(b_j\bar{E}_j - 1)} = \frac{\exp\left(\frac{\ln\omega_j - a_j}{\ln\lambda_{j,t}}\right)}{\left(b_j\exp\left(\frac{\ln\omega_j - a_j}{\ln\lambda_{j,t}}\right)\bar{E}_j - 1\right)}$$ (see eqns. S6 and S14).

To assess how well Eq. S1 with the modification in ω_j, i.e.,

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1 + \sum_{l=1}^{s}\alpha_{jl}N_l\right)^{\exp(a_j + b_j \ln\lambda_{j,t})}}, \qquad \text{(Eq. S4)}$$

is able to reflect the population dynamics of mechanistic models we conducted some simulations. We used a variant of Eq. S2 that includes interacting species,

$$S_{j,t+1} = \sigma_j\left(1 - g_{j,t}\right)S_{j,t} + \frac{g_{j,t}\varphi_j}{1 + \sum_l \alpha_{jl} g_{l,t} S_{l,t}} S_{j,t}. \qquad \text{(Eq. S5)}$$

In the simulations $g_{j,t}$ was allowed to change randomly over time assuming a uniform distribution between 0.7 and 1. φ_j was set to 30 for all species. The simulation was performed for three species sp1, sp2 and sp3 with σ_j values of 0.3, 0.15 and 0 respectively (the seed bank was set to relatively small numbers following unpublished measurements by V. Zepeda at the study site, Appendix S4). The remaining parameters are reported on Table S1. The simulation was conducted for nine annual transitions, recording the number of germinated species each year in 2000 quadrats. With the simulated data we fitted Eq. S4 by means of maximum likelihood using bbmle with the BFGS method, and assuming a normal error. As starting values we used 1000 latin hypercube samples obtained from package lhs (Carnell 2012), and kept the solution that provided the best fit.

Table S1. Estimated intrinsic growth rates ($\lambda_{j,t}$) and per-capita competition effects of species *l* on species *j* (α_{jl}).

	Seed bank model			Phenomenological model		
	Intrinsic growth rate					
time	sp1	sp2	sp3	sp1	sp2	sp3
1	25.6	27.9	28.0	33.2	30.7	27.4
2	23.7	21.8	25.7	31.8	24.3	25.1
3	23.9	25.2	28.9	32.8	29.4	28.3
4	27.4	24.9	23.6	37.7	28.3	23.1
5	24.6	29.0	28.6	32.5	33.0	28.0
6	21.5	26.5	21.2	29.3	29.1	20.8
7	26.3	22.8	24.4	37.0	25.5	23.9
8	23.5	23.3	26.2	31.5	26.9	25.7
9	21.8	29.1	26.3	30.2	33.3	25.7

	α values					
focal species	associated species			associated species		
	sp1	sp2	sp3	sp1	sp2	sp3
sp1	1.00	0.50	0.00	1.54	0.74	0.01
sp2	0.50	2.00	1.00	0.57	2.28	1.13
sp3	0.25	0.25	1.00	0.24	0.24	0.97

The estimated $\lambda_{j,t}$ values had a high correlation with the germination probabilities ($r = 0.952$, 0.981 and 1.000 for sp1, sp2 and sp3, respectively). The α_{jl} used to generate the data and those estimated by maximum likelihood were also highly correlated ($r = 1.000$). Nevertheless, both $\lambda_{j,t}$ and α_{jl} were larger than expected in the fitted model, and the difference increased with σ_j (Table S1). However, large $\lambda_{j,t}$ increase the growth rate of the population, whereas large α_{jl} diminish it, which may lead to a compensation. To assess if this happens, we plotted the population growth estimated from equations S4 and S5. The results are very similar (Fig. S2), indicating that the overestimation of $\lambda_{j,t}$ and α_{jl} does not affect the population dynamics. Actually, α_{jl} needs to be increased in Eq. S4 if $\omega_j < 1$ (which is in fact what occurs, in agreement with Fig. S1) in order for competition to have an effect on the population similar to that observed in Eq. S5.

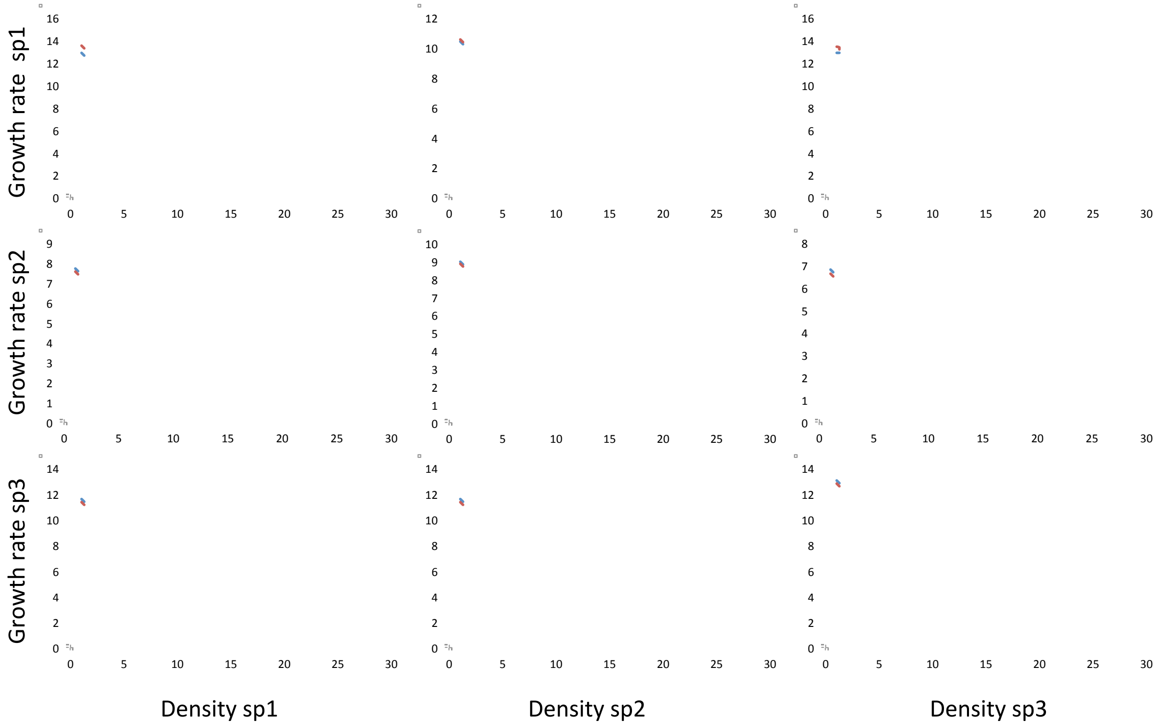

Fig. S2. Comparison between the growth rates from a mechanistic seed bank model (blue) and the phenomenological model used in this study (red).

R code for simulation and fitting

```
##SIMULATION OF A POPULATION WITH SEED BANK DYNAMICS
##surv=survival probability in the seed bank, g1= lower bound of germination
probability,
##g2=upper bound of germination probability, fec=number of seeds produced per
adult,
##alfa=competition coefficient,x=initial number of seeds, sig=std. dev. of
sampling error
##iter=number of iterations

seed=function(surv,g1,g2,fec,alfa,x){
        x=runif(1000,0,x)
        ts=matrix(NA,ncol=11,nrow=1000)
        tss=matrix(NA,ncol=2,nrow=10000)
        for(i in 1:11){
                g=runif(1,g1,g2)
                ts[,i]=g*x
                x=surv*(1-g)*x+g*fec*x/(1+alfa*g*x)
        }
        for(i in 1:1000){
                vec=ts[i,]
                tss[((i-1)*10+1):(i*10),]=cbind(vec[1:10],vec[2:11])
        }
        tss
}
```

```r
##SIMULATION OF A POPULATION WITH PERENNIAL INDIVIDUALS
##s1= lower bound of adult survival probability, s2= lower bound of adult
survival probability,
##fec=adult fecundity, alfa, x, sig and iter as before.
long=function(s1,s2,fec,alfa,x){
	x=runif(1000,0,x)
	ts=matrix(NA,ncol=11,nrow=1000)
	tss=matrix(NA,ncol=2,nrow=10000)
	for(i in 1:11){
		surv=runif(1,s1,s2)
		ts[,i]=x
		x=x*surv+fec*x/(1+alfa*x)
	}
	for(i in 1:1000){
		vec=ts[i,]
		tss[((i-1)*10+1):(i*10),]=cbind(vec[1:10],vec[2:11])
	}
	tss
}



##FUNCTION TO ESTIMATE LOG LIKELIHOOD USING THE MODEL WITH OMEGA
logL=function(ts,lambda,alfa,omega,sig){
	omega=exp(omega)
	lambda=exp(lambda)
	alfa=exp(alfa)
	sig=exp(sig)
	x=ts[,1]
	y=ts[,2]
	mu=lambda*x/(1+alfa*x)^omega
	-sum(dnorm(y,mean=mu,sd=sig,log=T))
}

##FIT THE MODEL
library(bbmle)

tsseed=seed(.75,.9,.9,5,.5,20)
mod=mle2(logL,start=list(lambda=1.1,alfa=0,omega=-.4,sig=-
3),data=list(ts=tsseed),method="SANN")
mod=mle2(logL,start=list(lambda=coef(mod)[1],alfa=coef(mod)[2],omega=coef(mod)[3]
,sig=coef(mod)[4]),data=list(ts=tsseed))
mod

tslong=long(0.5,0.5,2,.5,20)
mod=mle2(logL,start=list(lambda=2,alfa=5,omega=-1.3,sig=-
3),data=list(ts=tslong),method="SANN")
mod=mle2(logL,start=list(lambda=coef(mod)[1],alfa=coef(mod)[2],omega=coef(mod)[3]
,sig=coef(mod)[4]),data=list(ts=tslong))
mod
```

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Supporting Information. Zepeda, V., and C. Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*.

Appendix S2. Constancy of per capita interaction coefficients

One of the conditions for the storage effect is the covariance between environment and competition. In our model, this can occur if the number of competitors increases in years that are favourable to the focal species. While the model does not include any terms that explicitly capture such behaviour, it could potentially arise because the population growth rates (λ, which were used as proxies of the quality of the years) were positively correlated between species, indicating similar responses to the environment. Nevertheless, the extremely small covariances observed suggest that this was not the case.

Our model may be missing an important source of covariation between environment and competition, which is variable per-capita competition coefficients α over time. If in some years the individuals of a species take more resources, we would expect them to have a larger competitive effect on their neighbours and their population to grow rapidly. Thus we expect α to increase with λ, and thus it makes sense to consider the following model:

$$N_{j,t+1} = \frac{\lambda_{j,t} N_{j,t}}{\left(1 + \sum_{l=1}^{s} \left[\lambda_{j,t} \alpha_{jl}^{w}\right] N_{j,t}\right)^{\exp(a_j + b_j \ln \lambda_{j,t})}} \qquad \text{(Eq. S1)}$$

where $N_{j,t,i}$ is the number of individuals of species *j* at time *t* in the *i* square, $\lambda_{j,t}$ is the intrinsic growth rate (population growth rate when there is no competition) at time *t*, α_{jl} is the per capita competition effects of species *l* on species *j*, parameters *w*, a_j and b_j are constants. *s* is the number of associated species. Note that the term in square brackets corresponds to a competition coefficient that increases with λ. The constant *w* modulates the effect of competition on λ. If $w = 0$, then the per capita competitive effects are constant over time, and we have the model that we analyse in the main text.

In Eq. S1, environment-competition covariance arises naturally, but not in our model with $w = 0$. The use of Eq. S1 may be appealing, but it renders the estimation procedure impracticable because then all species and coefficients have to be fitted simultaneously. This is a huge estimation problem that requires computational and statistical tools that are still unavailable. This implies an important issue: Are our very small covariance estimates a reflection of what is going on in nature? Or are they an artefact of not using a model such as Eq. S1?

To assess if there is any evidence that competition (i.e., α values) change over time we used simulation approach. We simulated ten transitions for three species in 100 squares where the initial densities of the three species were set at random. To include environmental variation in the simulations, in every transition a different λ was obtained from a normal distribution for each species. In different simulations we changed the correlations between the population growth rates of the three species (Table S1). We assessed the effects of different correlations because, as indicated above, they may have an indirect effect on environment-competition covariance. We used the simulated λ values to project the population dynamics in each square over time assuming that the population dynamics are ruled by Eq. S1. Importantly, in different simulations we used different *w* values ranging from 0.1 to 1.9, *b* values between 0 and 0.8. The values of the remaining parameters were the same in every simulation and are shown in Table S1. In total we ran 350 simulations, one for each combination of *b* (5 possible values), *w* (10 possible values) and correlation (7 possible values).

Table S1. Values of the controlled parameters.

Parameters	Values			
a	Fixed in 0			
b	0, 0.2, 0.4, 0.6, 0.8			
Correlation between lambdas	-0.5,-0.3,-0.1,0.1,0.3,0.5,0.7			
Mean of the lambdas	1			
Standard deviation of lambdas	0.5			
w	0.1,0.3,0.5,0.7,0.9,1.1,1.3,1.5,1.7,1.9			
Matrix of α		sp1	sp2	sp3
	sp1	0.522	0.225	0.642
	sp2	0.758	0.141	0.096
	sp3	0.305	0.685	0.878

Once the time series of population abundances were generated, we fitted the model

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1+\sum_{l=1}^{s}\alpha_{jl}N_{t,l}\right)^{\exp(a+b\ln\lambda_{j,t})}} \qquad \text{(Eq. S2)}$$

for each species separately. This is the model that we used in the main text with $w = 0$. This means that for each species we estimated ten $\lambda_{j,t}$, three competition coefficients α_{jl}, a_j, and b_j.

Parameter estimation was performed through maximum likelihood by using the mle2 function of bbmle package in R (Bolker and Team 2012) and assuming normal error. We employed a Latin Hypercube by using Random LHS package in R (Carnell 2012) with 150 initial points for the model fitting to get a better sampling of the likelihood surface and increase the probabilities of finding a global maximum. For this step we set the same boundaries reported in Appendix S3 (Model fitting) to the parameter values to keep them inside what can be considered biologically sound (Appendix S3: Table S1).

Once we had the "true" models (the ones from which the data were generated) and the fitted models we compared them to see if there were any patters in the fitted estimates that could inform us about the nature of the underlying processes.

We found a positive correlation between the estimated values of *b* and the underlying values of *w* (Spearman's *rho*=0.55, *P*<0.001, Fig. S2.1) irrespective of the correlation between λ. Data generated from small values of *w* also show small values of fitted parameter *b*. There was also, as expected, a positive correlation between estimated and the "real" *b*; after removing this trend, the correlation between the estimated values of *b* and f *w* was still large (Spearman's *rho*=0.62, *P*<0.001).

Most of the *b* values estimated for our species and reported in the main text are close to zero. This is consistent with very low *w* values and thus indicates that per capita competition coefficients are relatively constant over time. A *w* value near zero would also indicate that the model that we used is reasonably accurate, and that a lack of environment-competition covariance is not likely to be solely a model's artefact.

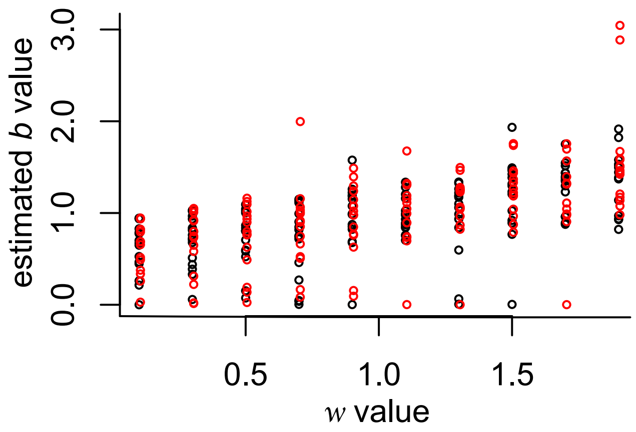

Fig. S1. Correlation between *w* values and the estimated *b* values.

Interaction strengths

One assumption of our model is that per capita interaction strengths (α) are constant. These constants may shift over the life cycle, as the effects of neighboring plants on the focal species change with plant size (Miriti 2006). If plants are larger on some years or sites, our assumption would not be valid. Here we assess possible neglected changes in interactions throughout the life cycle by analyzing the change of interaction coefficients. In a previous experiment (Zepeda and Martorell 2019), we quantified the strength of positive and negative effects on the survival and growth of nine of the 19 study species. The field experiment was carried out with four associated species and five levels of density of associated species. To test whether the size of individuals affects the strength of competition we performed a GLMM with a binomial link for survival and identity for growth. The fitted model for survival was:

$$\eta_{s,j} = \beta_{0,j} + \beta_{1,j} d_j + \beta_{2,j} \ln T_t + \beta_{3,j} \ln T_t{:}d_j + \varepsilon_p + \varepsilon_t \qquad \text{(Eq. S3)}$$

for growth:

$$\ln T_{t+1,j} = \beta_{0,j} + \beta_{1,j} d_j + \beta_{2,j} \ln T_t + \beta_{3,j} \ln T_t{:}d_j + \varepsilon_p + \varepsilon_t, \qquad \text{(Eq. S4)}$$

where $\eta_{s,j}$ is the logit of the survival probability of focal species in the presence of species j; $T_{t,j}$ is the size at time t of an individual in a species-j plot; d is the density of associated species j. $\beta_{0,j}$ is the survival probability when the species j is not present; β_1 is the effect of species j on the performance of the focal species or the interaction strength; $\beta_{2,j}$ is the magnitude of the effect of plant size on growth or survival; $\beta_{3,j}$ is the change in the strength of the interaction as a result of the size of the individual. ε_{p} is the random effect of the plot and ε_{t} is the random effect of the measuring date. For Eq. S3 $\beta_{0,j,}$ $\beta_{1,j,}$ $\beta_{2,j}$ and $\beta_{3,}$ have the same meaning that Eq. S4 with the exception that the time period correspond to one month.

We did not find significant changes in the type and strength of the interaction as a result of the size of the individual during survival (Table S2). When we assess for interactions shifts on plant growth by looking at coefficient $\beta_{3,j}$, only two were significant. These results suggest that, in general, the sign and intensity of interactions among plants do not shift with plant size. Moreover, it is expected to observe the same patterns on plant fitness, as survival and growth are two important components of it.

Table S2. Estimates and *P* values of interaction shifts (parameter $\beta_{3,j}$). Numbers in bold were significative.

Code	Species	Estimate	*P* value	Estimate	*P* value
		Survival		Growth	
aa	*Aristida adscensionis*	-0.0058	0.9276	-0.0176	**0.0406**
bc	*Bouteloua chondrosioides*	0.0630	0.4491	0.0043	0.2887
fp	*Florestina pedata*	-0.0894	0.1366	0.0084	0.1736
hp	*Heterosperma pinnatum*	-0.0020	0.9182	-0.0130	**0.0282**
mk	*Microchloa kunthii*	0.0253	0.8565	-0.0176	0.1739
st	*Sporobolus tenuissimus*	-0.7328	0.3893	0.0076	0.2377
se	*Stevia ephemera*	0.0288	0.3689	0.0061	0.0822
tm	*Tagetes micrantha*	0.0221	0.2115	-0.0004	0.3136
ta	*Thymophylla aurantiaca*	-0.4500	0.2833	0.0116	0.0677

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Supporting Information. Zepeda, V., and C. Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*.

Appendix S3. Model fitting

The movement of seeds across sampling units may bias the estimates of interaction coefficients (α_j) (Freckleton and Watkinson 2000) . Thus, during the parameter estimation process, seed dispersal was included in the model. To do so, we define the number of individuals of the j^{th} species that are produced or survive from time t to t +1 in the l^{th} 0.1 × 0.1 m square, $N'_{j,t+1,l}$, as:

$$N'_{j,t+1,l} = \frac{\lambda_{j,t} N_{j,t,l}}{\left(1 + \sum_k \alpha_{j,k} N_{t,k,l}\right)^{\exp(a_j + b_j \ln \lambda_{j,t})}} \qquad \text{(Eq. S1)}$$

(see Eq. 1 in the main text). Of these individuals, a fraction m_j leaves the l^{th} square, arrives to others in the 1 m^2 quadrat, and becomes established at time t + 1. Of course, those "immigrating" individuals come from seeds and are not previously established plants that survive to time t + 1. In preliminary versions of the analysis, we considered that seeds would have a greater probability of landing in nearby squares than in distant ones. However, in those cases, the procedure resulted in extremely large values of $\lambda_{j,t}$ and m_j, and inordinately long dispersal distances. This effectively resulted in just a few seeds remaining within the 1 m^2 quadrat and in very flat dispersal kernels, suggesting that all the seeds produced within a quadrat had the same probability of arriving to any 0.1 × 0.1 m square in it. Thus, in the final version of the model, we assumed that the seeds produced in a square were equally distributed among all the squares in a quadrat. In this version of the model $\lambda_{j,t}$ and m_j values were much smaller and biologically plausible.

We must bear in mind that we only sampled 20 squares in each quadrat, that is, one fifth of the 100 0.1 × 0.1 m squares that are comprised in the whole quadrat. Thus, the number of seeds S_j that move across squares in a 1 m^2 quadrat and become established is

$$S_j = 5 m_j \sum_{l=1}^{20} N'_{j,t+1,l} \qquad \text{(Eq. S2)}$$

(Note that we are assuming that no seeds leave the quadrat, or that the number of seeds that emigrate is equal to the ones that immigrate. This may be expected if the community in the vicinity of the quadrat is more or less similar to that inside it). Under the assumption that seeds are equally distributed among all the squares, the number of seeds that arrive to a square would be

$$\frac{S_j}{100} = m_j \frac{\sum_{l=1}^{20} N'_{j,t+1,l}}{20} = m_j \overline{N'_{j,t+1}} , \qquad \text{(Eq. S3)}$$

where $\overline{N'_{j,t+1}}$ is the value of $N'_{j,t+1,l}$ averaged over the 20 sampled squares. Thus, the number of individuals of the j^{th} species in the l^{th} square at time t + 1 is

$$N_{j,t+1,l} = (1-m_j)N'_{j,t,l} + m_j\overline{N'_{j,t+1}}. \quad \text{(Eq. S4)}$$

Parameter estimation was performed through maximum likelihood using ADMB program (Fournier et al. 2012). From previous work, we know that at the study site the distribution of $N_{j,t+1,l}$ is a negative binomial (Martorell and Freckleton 2014). The ADMB code used for fitting Eq. S4 is appended below. In high-dimensional non-linear models, finding the maximum-likelihood parameters poses a number of problems: given the large number of parameters involved, and thus the wide variations allowed in the shape of the fitted model, a few data with a large leverage tend to twist the fitted model away from the general behaviour of the remainder of the dataset (overfitting); the likelihood surface is complex and has many maxima, but only a subset of these are biologically plausible; and finding appropriate initial values for the optimization process is daunting. To solve these issues, we followed three strategies: (1) we set boundaries to the parameter values to keep them inside what can be considered biologically sound; (2) we used a two-step optimization algorithm; and (3) we chose several initial values and selected those that resulted in the maximum likelihood.

Parameter boundaries

Some parameters must be positive in order to make sense biologically. This is the case of $\lambda_{j,t}$, $\alpha_{j,k}$, and the overdispersion parameter of the negative binomial distribution. In those cases, we used an exponential function to keep them positive. We also forced parameter b_j to be positive because in preliminary simulations none of the species with negative b_j values were able to coexist in the community, suggesting that such values do not describe the observed dynamics appropriately. As can be seen in Appendix S5, subadditivity is possible when $0 < b_j < \frac{1}{\overline{E}_j}$. Thus, positive values of b_j favour coexistence by storage effect as it allows buffered population growth. It has been argued that this is the situation that should commonly be observed in nature (Chesson 2000). The dispersal probability m_j was bounded between 0 and 1 by means of a logistic (inverse log-odds) transformation. ADMB performs better if the parameters are bounded to a given interval (Fournier et al. 2012). To define its limits, we consulted the values observed in a previous work conducted at the study site (Martorell and Freckleton 2014). The boundaries that we used were much larger than the observed intervals to grant that they contained the best solution (Table S1).

Table S1. Parameter boundaries. The previously observed values for each parameter come from Martorell and Freckleton (2014). We report their mean and 0.05 – 0.95 quantiles (in parentheses). The boundaries set during the fitting procedure are reported in the column "parameter boundaries". In the case of parameters that had to be positive restricted to the 0–1 interval, we used exponential or logistic transformations, so the intervals that were provided to the optimization algorithm are shown in the column "transformed boundaries".

	Previously observed	Parameter boundaries	Transformed boundaries
$\lambda_{j,t}$	1.88 (0.41 – 6.23)	0.22 – 20.08	-1.5 – 3.0

$\alpha_{j,k}$	0.38 (0.00 – 1.39)	0.00 – 148.41	-10.0 – 5.0
a_j	NA	-1.00 – 1.00	-1.0 – 1.0
b_j	NA	0.00 – 1.00	-10.0 – 0.0
m_j	0.59 (0.26 – 0.76)	0.00 – 1.00	-10.0 – 10.0
overdispersion parameter	1.63 (0.46 – 4.60)	0.01 – 148.41	-5.0 – 5.0

During the fitting, it was observed that in many cases extremely large $\lambda_{j,t}$ values were estimated for years in which rainfall was most scarce and many species performed poorly. This would mean that populations could grow inordinately during very adverse periods, which is most likely to be incorrect. The reason for those poor fits was related to the power of the competition term in Eq. S1, $\exp(a_j + b_j \ln \lambda_{j,t})$. A strong population decline from time t to $t + 1$ can be either caused by a poor year with a low $\lambda_{j,t}$ or by a strong competition, which would result from a very large $\lambda_{j,t}$ (See Eq. S1). This makes it difficult for the optimization algorithm to tell between those two alternatives. To solve this problem, we noted that in most plant populations, the power of the competition term is close to one (Freckleton and Watkinson 2002), or, in terms of our model, $\exp(a_j + b_j \ln \lambda_{j,t}) \approx 1$. Thus, large deviations from this value do not seem biologically plausible. To avoid such results, we penalized the log-likelihood by adding a penalty P (Fournier et al. 2012)

$$P = \sum_t \exp\left(-15 + 30\left(a_j + b_j \ln \lambda_{j,t,l}\right)^2\right). \qquad \text{(Eq. S5)}$$

This penalty causes the log-likelihood to be small if $\exp(a_j + b_j \ln \lambda_{j,t}) < 0.05$ or if $1.6 < \exp(a_j + b_j \ln \lambda_{j,t})$, at least for one year t (Fig. S1). This causes models with power values very different from one to be rejected. Setting this restriction solved the problem of large $\lambda_{j,t}$ values in ostensibly bad years, and provided good overall estimates. We penalized the log-likelihood only in the first part of the model optimization.

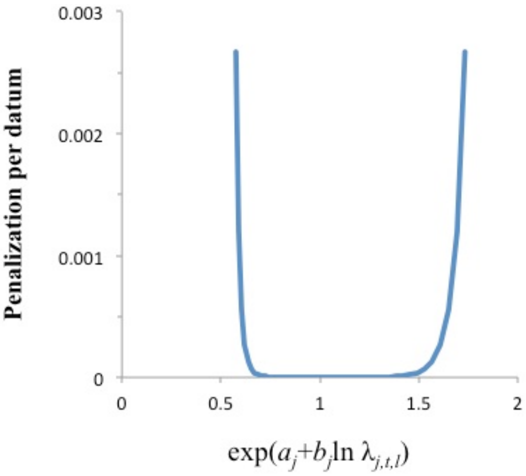

Fig. S1. Penalty added to the log-likelihood depending on the value of the power of the competition.

Two-step optimization

Fitting models in two steps aids in keeping the parameters within biologically plausible limits and finding the maximum likelihood solution, allowing for a better control of the search for the best fitting parameters (Fournier et al. 2012). Because intraspecific interactions are the main determinants of population dynamics at the study grassland (Martorell and Freckleton 2014), in the first step we estimated preliminary values for each species in isolation. More specifically, we estimated 17 parameters: 12 $\lambda_{j,t}$ and parameters a_j and b_j, α_{jj} and m_j, plus the overdispersion parameter of the negative binomial distribution. In the second step of the optimization, the parameters obtained in the first step are usually kept unchanged, and the remaining parameters (in this case, interspecific interaction coefficients) are fitted. Nevertheless, the inclusion of new parameters in the second step may somehow affect the ones from the first step. Therefore, in the second step we allowed parameters a_j, b_j and $\lambda_{j,t}$ to move ±1/3 of the preliminary values that were estimated in the first step. The values of m_j and the overdispersion parameter were left completely free. The penalty on the log-likelihood was not included in this second step.

Multiple initial values

When the likelihood surface is complex, there is no warranty that the global maximum is found, instead of a local one. Which maximum is reached depends on the initial values provided for optimization. In order to increase the probabilities of finding the global maximum, we employed a Latin hypercube to have a better sampling of the parameter space. To this, we used the Latin Hypercube Sampling package in R (Carnell 2012) with 1000 initial points for the model fitting in the first step and 500 initial points for the second one.

References

Carnell, R. 2012. lhs: Latin Hypercube Samples. Page R package

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Sotfw. **27**:233-249.

Freckleton, R. P. and A. R. Watkinson. 2000. On detecting and measuring competition in spatially structured plant communities. Ecol. Lett. **3**:423-432.

Freckleton, R. P. and A. R. Watkinson. 2002. Are weed population dynamics chaotic? Journal of Applied Ecology **39**:699-707.

Martorell, C. and R. Freckleton. 2014. Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage. Journal of Ecology **102**:74-85.

ADMB code for the first step of optimization

```
GLOBALS_SECTION

  #include <admodel.h>
  #include <df1b2fun.h>
  #include <adrndeff.h>
  #include <fvar.hpp>
  #include <admb_messages.h>
```

```
DATA_SECTION

init_int n; //Number of squares in quadrats where the focal species was present
init_int s; //Number of species in the data set (in this step s=1, but the code is already prepared to include
//the associated species in the second step)
init_matrix dat(1,n,1,13+s); //Read data matrix
matrix maty(1,n,1,12); //0 and 1 matrix of years
matrix N1(1,n,1,s); //Density all species in time t
vector N2(1,n); //Density of focal species in time t+1
vector foc(1,n); //Density of focal species in time t

PARAMETER_SECTION

//Population dynamics model parameters
init_bounded_vector lam(1,12,-1.5,3); //12 λi,t (ln)
init_bounded_vector alfas(1,s,-10,5); //Intraspecific competition coefficient (αii) (ln)
init_bounded_number a(-1,1); //Parameter aj
init_bounded_number b(-10,0); //Parameter bj (ln)
init_bounded_number disp(-5,5); //Overdispersion parameter of the negative binomial distribution (ln)
init_bounded_number mig(-10,10); //fraction of seeds that leaves a square (logit)
vector lambda; //Product of vector lam and maty. contains the appropriate lambda for each year
vector numerator; //numerator of Eq. S1
vector denominator; // denominator of Eq. S1
vector mu;//Population growth rate after accounting for competition

//Dispersal model parameters
number m; //Fraction of seeds that leaves the square (mj)
vector semi(1,n); // Number of seeds that leave each square
number semprom; //Average number of seeds that arrive to a square in a quadrat
vector subsemi(1,20); //Number of seeds that leave each square in a quadrat

//Log-likehood
vector cast(1,n); //Vector for penalizing the likelihood
objective_function_value log_likelihood;


PRELIMINARY_CALCS_SECTION
//Extract observational data
 for(int i=1;i<=12;i++){
                maty.colfill(i,extract_column(dat,i));
     }
 for(int i=1;i<=s;i++){
     N1.colfill(i,extract_column(dat,i+12));
     }
 N2=extract_column(dat,13+s);
 foc=column(dat,13);

  PROCEDURE_SECTION

//To model the population growth rate when there is competition
lambda=maty*mfexp(lam);
numerator=elem_prod(lambda,foc);
denominator= pow(1+N1*mfexp(alfas), mfexp(a+mfexp(b)*log(lambda)));
mu=elem_div(numerator,denominator);

m=1/(1+mfexp(-mig)); //Calculate the fraction of seeds that leaves the square
semi=m*mu;
```

```
//Calculates the average number of seeds that arrive to a square in each quadrat. Note that semi now becomes
//the number of seeds that ARRIVE to each square.
 for(int i=1;i<=n/20;i++){
   for(int j=(i-1)*20+1;j<=i*20;j++){
     subsemi[j-(i-1)*20]=semi[j];
     }
   semprom=sum(subsemi)/20;
   for(int j=(i-1)*20+1;j<=i*20;j++){
     semi[j]=semprom;
     }
   }

 mu=(1-m)*mu+semi;//Number of seeds  or individuals that remains in the square plus those that arrive
 cast=mfexp(-15+30*square(a+mfexp(b)*log(lambda))); //Penalty for the likelihood function
log_likelihood=dnbinom(N2,mu,mfexp(disp))+sum(cast); //Penalized Log likelihood function
```

ADMB code for the second step of optimization

(No comments are added to code lines that are identical to the first step)

```
GLOBALS_SECTION

  #include <admodel.h>
  #include <df1b2fun.h>
  #include <adrndeff.h>
  #include <fvar.hpp>
  #include <admb_messages.h>

DATA_SECTION

init_int n;
init_int s;

//Population model dynamics parameters
////Read variables for the estimated parameters in the first step of the model fitting
init_number l1a;
init_number l2a;
init_number l3a;
init_number l4a;
init_number l5a;
init_number l6a;
init_number l7a;
init_number l8a;
init_number l9a;
init_number l10a;
init_number l11a;
init_number l12a;
init_number preaa;
init_number preba;
init_number l1b;
init_number l2b;
init_number l3b;
init_number l4b;
init_number l5b;
init_number l6b;
```

```
init_number l7b;
init_number l8b;
init_number l9b;
init_number l10b;
init_number l11b;
init_number l12b;
init_number preab;
init_number prebb;

init_matrix dat(1,n,1,13+s);
matrix maty(1,n,1,12);
matrix N1(1,n,1,s);
vector N2(1,n);
vector foc(1,n);


PARAMETER_SECTION
```

// For the parameters a_i, b_i and $\lambda_{i,t}$ we allowed them to move ±1/3 of the preliminary values estimated in the first step

```
init_bounded_number lam1(l1a,l1b);
init_bounded_number lam2(l2a,l2b);
init_bounded_number lam3(l3a,l3b);
init_bounded_number lam4(l4a,l4b);
init_bounded_number lam5(l5a,l5b);
init_bounded_number lam6(l6a,l6b);
init_bounded_number lam7(l7a,l7b);
init_bounded_number lam8(l8a,l8b);
init_bounded_number lam9(l9a,l9b);
init_bounded_number lam10(l10a,l10b);
init_bounded_number lam11(l11a,l11b);
init_bounded_number lam12(l12a,l12b);
init_bounded_number a(preaa,preab);
init_bounded_number b(preba,prebb);

//The following parameters were estimated in this step of the model fitting with out any restriction
init_bounded_vector alfas(1,s,-10,5);
init_bounded_number disp(-5,5);
init_bounded_number mig(-10,10);

vector lam(1,12);
vector lambda;
vector numerator;
vector denominator;
vector mu;

number m;
vector semi(1,n);
number semprom;
vector subsemi(1,20);
objective_function_value log_likelihood;


PRELIMINARY_CALCS_SECTION

for(int i=1;i<=12;i++){
     maty.colfill(i,extract_column(dat,i));
```

```
     }
 for(int i=1;i<=s;i++){
     N1.colfill(i,extract_column(dat,i+12));
     }
 N2=extract_column(dat,13+s);
 foc=column(dat,13);


PROCEDURE_SECTION

 m=1/(1+mfexp(-mig));
 semi=m*mu;

//Fill a vector with the lambda values
 lam(1)=lam1;
 lam(2)=lam2;
 lam(3)=lam3;
 lam(4)=lam4;
 lam(5)=lam5;
 lam(6)=lam6;
 lam(7)=lam7;
 lam(8)=lam8;
 lam(9)=lam9;
 lam(10)=lam10;
 lam(11)=lam11;
 lam(12)=lam12;

lambda=maty*mfexp(lam);
 numerator=elem_prod(lambda,foc);
 denominator= pow(1+N1*mfexp(alfas), mfexp(a+mfexp(b)*log(lambda)));
 mu=elem_div(numerator,denominator);

 for(int i=1;i<=n/20;i++){
    for(int j=(i-1)*20+1;j<=i*20;j++){
       subsemi[j-(i-1)*20]=semi[j];
       }
    semprom=sum(subsemi)/20;
    for(int j=(i-1)*20+1;j<=i*20;j++){
       semi[j]=semprom;
       }
    }

 mu=(1-m)*mu+semi;
log_likelihood=dnbinom(N2,mu,mfexp(disp));//(not-penalized) Log likelihood function
```

Supporting information. Zepeda, V. and C., Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*.

Appendix S4: Statistical considerations on model fitting

Measurement error

When time series of population densities are analysed, the issue of measurement error becomes important because it causes intraspecific competition to be overestimated (Freckleton et al. 2006). State-space models should solve the problem by considering measurement error explicitly. They do so by recognising that data reflect the outcome of two stochastic processes: *process error*, which comprises the stochastic factors that determine the actual dynamics of the population (*e.g.,* demographic stochasticity, disturbances, climatic fluctuations), and *measurement error*, which does not determine the dynamics but still affect our recorded data (*e.g.,* counting errors, misidentification of species) (Durbin and Koopman 2012). Nevertheless, recent work shows that, under conditions frequently met in population ecology, state-space estimates may be unreliable even when based on simple models (Knape 2008, Auger-Méthé et al. 2016). Thus, such statistical approach holds little promise when applied to our non-linear, high-dimensional model.

We took several precautions in the field to reduce error to the minimum: (1) Data are collected some 4–5 months after the rainy season has begun. By then, most plants are reproducing and are well developed, making identification straightforward. (2) Most data are directly captured in the field to a digital device (a palm handheld or more recently a tablet) to minimise transcription errors. (3) The formats where data are recorded show the whole history of each 0.1 × 0.1 m square. This allows *in situ* detection and correction errors due to, for example, misidentification of perennial plants or individuals that grow exactly in the boundaries between squares. (4) The vast majority of squares have < 20 individuals, so they are very conspicuous and are hard to miss. Thus, we believe that measurement error may occur in no more than 10 % of our data (considering that one datum is the number of individuals of any species in one square), and that the magnitude of the errors would rarely be greater than ± 10 %.

Despite this, there are certainly some errors in the database, so the question remains of what effect could they have on our estimates. To address this issue, we conducted a series of simulations where measurement error was introduced in the time series with frequencies f (fraction of incorrect data) and magnitudes m (difference between the actual and the recorded figure) between 2 and 20 % (f and $m \in \{2,6,10,13,16,20\}$). The data for each simulation was generated as follows:

1) We chose three scenarios with two species each. The scenarios differed in the strength of subadditivity (b parameter) and in the ratio of intra to interspecific competition. In each scenario we simulated 1000 squares that were monitored for ten annual transitions. The intrinsic population growth rate λ for each species varied in each transition. We selected the intra and interspecific competition coefficients so we had a range from mild to strong competition, and from similar to very different intra- and interspecific coefficients α. We

also included cases with low and with high *b* values (Table S4.1). Parameter values were selected by a trial-and-error procedure so that both species were capable of persisting in at least half of the squares after ten transitions.

2) For each scenario we randomly assigned an initial density to each of the 1000 squares. We then simulated data using the equation

$$N_{i,t+1} = \frac{\lambda_{i,t} N_{i,t}}{\left(1+\alpha_{i,i} N_{i,t} + \alpha_{i,j} N_{j,t}\right)^{\exp\left(a_i + b_i \ln \lambda_{i,t}\right)}}, \qquad \text{(Eq. S4.1)}$$

(see main text). We added process error by choosing a random number from a negative binomial distribution with mean $N_{i,t+1}$. This number was then plugged back to the equation to obtain the population densities for the next year and so on, until ten annual transitions were completed.

3) Measurement error was then incorporated by selecting the data to be mismeasured with probability equal to a given error frequency, *f*. The selected data were then changed by a fraction *ε* of their correct value. The procedure is easier to understand with an example. Assume that we are using an error magnitude *m* = 20 %. We first obtained *ε* from a uniform distribution between 0.8 and 1.2 (*i.e.,* 1 ± 0.2; a different *ε* was used for each square). Second, assuming that for a particular square $\varepsilon = 1.13$ and $N_{i,t} = 10$, so we end up with a measured value of $N_{i,t} = 11.3$, which is of course impossible because no fractions of individual can be recorded (nor analysed using a negative binomial distribution for the error). To solve this problem, we set $N_{i,t} = 11$ with a probability of 0.7 (= 1 - 0.3, the non-integer portion of 11.3), and $N_{i,t} =$ 12 with a probability of 0.3.

Table S4.1. Parameters used in the three scenarios for simulating data. The ten λ value correspond to the intrinsic population growth rate for each annual transition, α correspond to the intra and interspecific competition coefficients, and *a* and *b* appear in the exponent in equation S4.1.

Param-eter	Scenario 1		Scenario 2		Scenario 3	
	Species 1	Species 2	Species 1	Species 2	Species 1	Species 2
λ_1	3.559	2.841	4.587	4.255	3.320	3.012
λ_2	1.321	10.051	3.296	6.483	2.161	5.207
λ_3	1.845	7.660	3.684	5.922	2.498	4.629
λ_4	18.967	9.582	8.012	6.381	6.856	5.100
λ_5	5.736	19.183	5.378	8.042	4.084	6.890
λ_6	9.486	15.974	6.359	7.566	5.078	6.365
λ_7	18.737	1.834	7.979	3.677	6.820	2.491
λ_8	2.062	1.041	3.824	3.045	2.621	1.949
λ_9	7.088	17.117	5.771	7.742	4.476	6.558
λ_{10}	1.960	4.763	3.760	5.054	2.564	3.767
α_{intra}	0.300	0.300	0.600	0.800	0.500	0.250

α_{inter}	0.250	0.250	0.500	0.400	0.250	0.125
a	0.010	0.300	-0.900	-0.700	-1.000	-1.000
b	0.010	0.010	0.600	0.500	0.300	0.400

Once the data had been generated, Eq. S4.1 was fitted by means of maximum likelihood using package bbmle (Bolker and R Development Core Team 2017). Two fits were conducted: one to the data without measurement error and another to the mismeasured data. The rate of error e_β of any given parameter in the model β was obtained as

$$e_\beta = \frac{\hat{\beta} - \beta_r}{\beta_r} \quad , \qquad \text{(Eq. S4.2)}$$

where $\hat{\beta}$ is the maximum-likelihood estimate obtained from the time series after including measurement error, and β_r is a reference value of the parameter, in this case the estimate of β obtained from the data without measurement error. The procedure was repeated 200 times for each combination of f and m. The error rates for each parameter were averaged over the 200 repetitions. The mean rates for the ten λ values of each species were also averaged. A positive value of e_β indicates a trend to overestimate a parameter when measurement error was included, whereas underestimations correspond to negative values. The value of e_β can be interpreted as the proportional change in a parameter caused by measurement error. Thus, $e_\beta = 0.25$ means that the parameter is inflated by 25 % of its real value.

In general, the frequency of errors had a greater effect on parameter estimation than their magnitude. There was a trend for λ to be slightly overestimated ($e_\beta < 0.08$), wheras a and b were less affected by measurement error ($|e_\beta| < 0.05$, with the exception of scenario 1, where large errors were produced for these parameters. It must be noted that the “real” values for these parameters in scenario 1 are extremely small, so tiny errors in estimation translate into huge differences when they are reported in a relative scale). Importantly, a and b were sometimes overestimated and others underestimated, indicating that there is no systematic bias (Fig. S4.1).

As expected, measurement errors affected the estimates of intraspecific competition. Error was relatively small in five out of the six species (each of the three scenarios comprises two species) ($|e_\beta| < 0.07$), but an overestimation of up to 25% was recorded in the sixth one (Fig. S4.1). However, there does not seem to be much room for bias there: depending on the scenario, the error was sometimes positive and others negative (Fig. S4.1).

Errors in interspecific competition estimates were positively correlated with those in intraspecific competition (Fig. S4.2). To determine how the magnitudes of error in intra and interspecific competition relate to each other as measurement error changes, we conducted type II regressions using package lmodel2 (Legendre 2018). Because of the way we are defining e_β, the intercept is necessarily zero, so we set the analysis so that the regression line passes through the origin. The slope is then equal to the ratio of errors in interspecific to intraspecific estimates. The slopes relating errors in both competition coefficients ranged from 0.96 to 1.14, suggesting a trend for interspecific competition to be slightly more overestimated than interspecific one, but the opposite also happened.

That estimation errors on both coefficients tend to be similar is important because it is the relationship between both forms of competition that determines coexistence (Chesson 2000). If, for instance, intraspecific competition were overestimated and interspecific competition underestimated, then our finding that fluctuation-independent niche differentiation is important at the study site could be spurious. However, this was not the case.

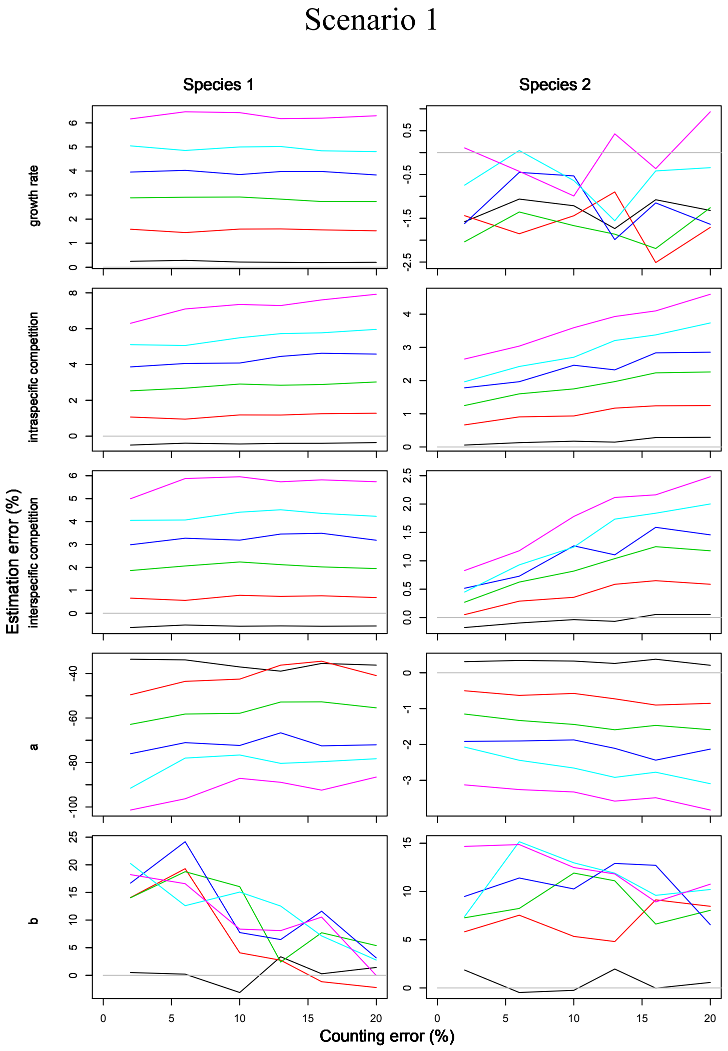

Figure S4.1. Mean error rate e_β (transformed into percent error) for different parameters in three scenarios. See table 1 for the parameter used to generate the data. Different lines correspond to different frequencies of measurement error: black 2%; red 6%; green 10 %; blue 13 %; cyan 16 %; and magenta 20 %.

Scenario 2

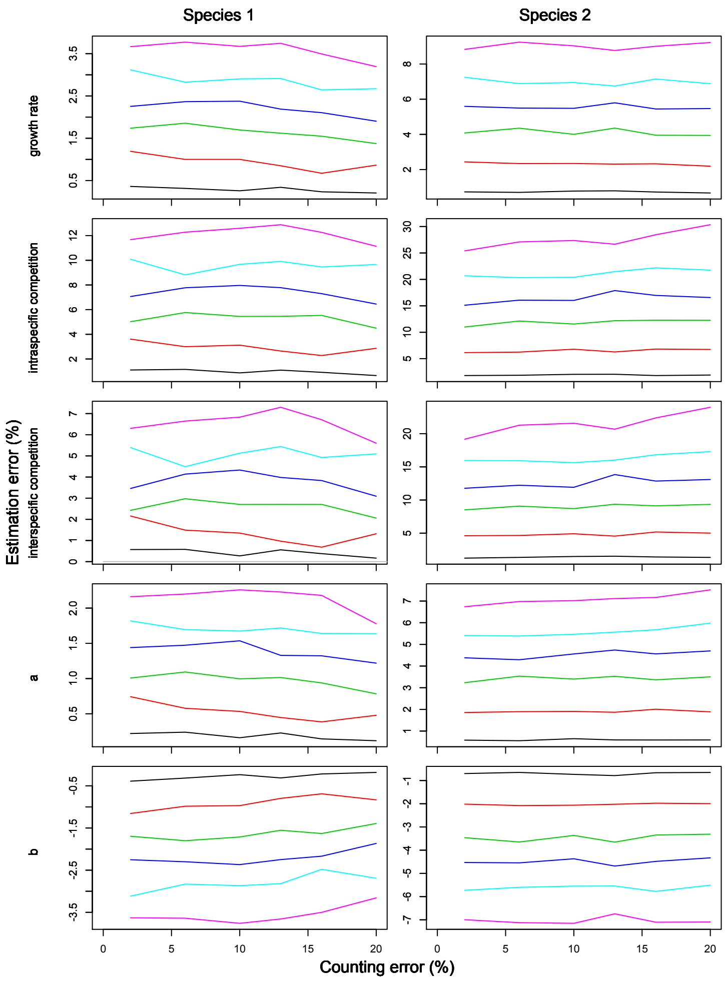

Figure S4.1 (cont.)

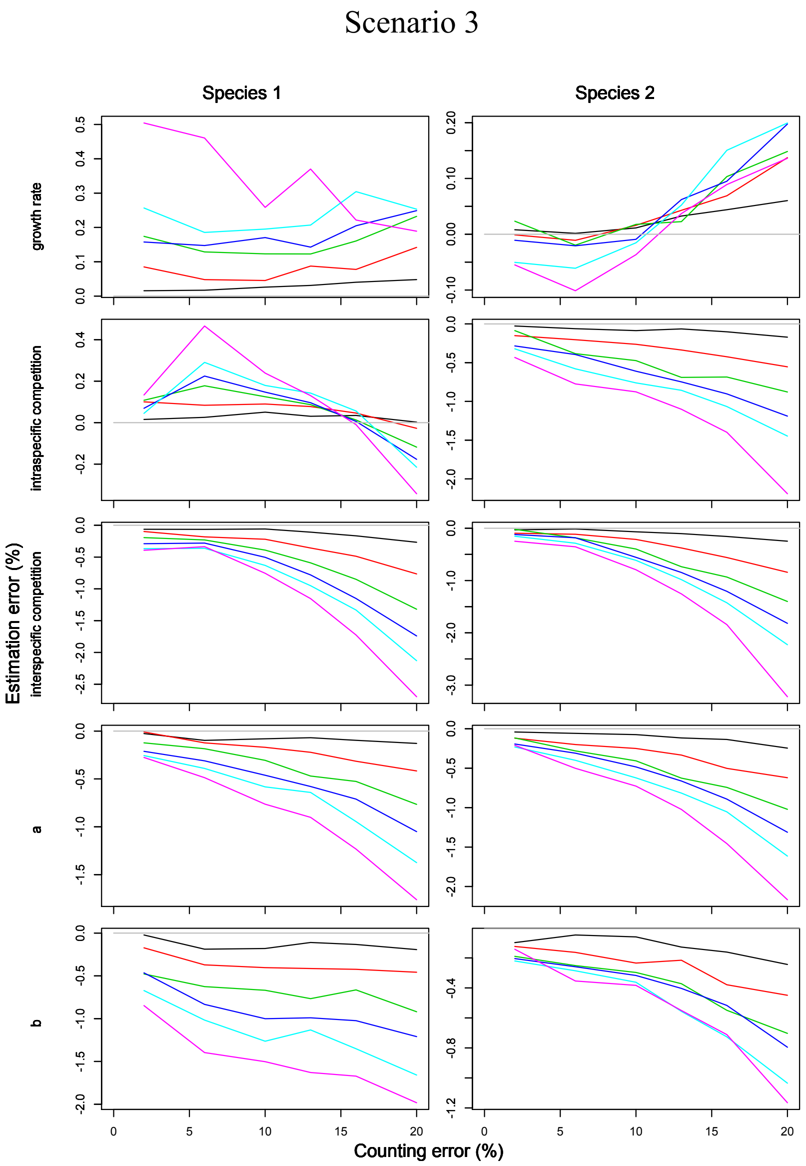

Fig. S4.1 (cont.)

Data coverage

The basis for our procedure to estimate interactions is the "response surface" experiment (Goldberg and Scheiner 2001). In that protocol, two interacting species are manipulated so as to produce every possible combination of their densities (Table S4.2 A). The response of each species to its own density (N_1) and that of the associated species' (N_2) is then recorded, and a function $f(N_1, N_2)$ is fitted by means of multiple regression. Some of the parameters in *f* can then be used as indicators of interaction strength. In our case *f* is the model in Eq. S4.1, and α are our measurements of *per capita* competition.

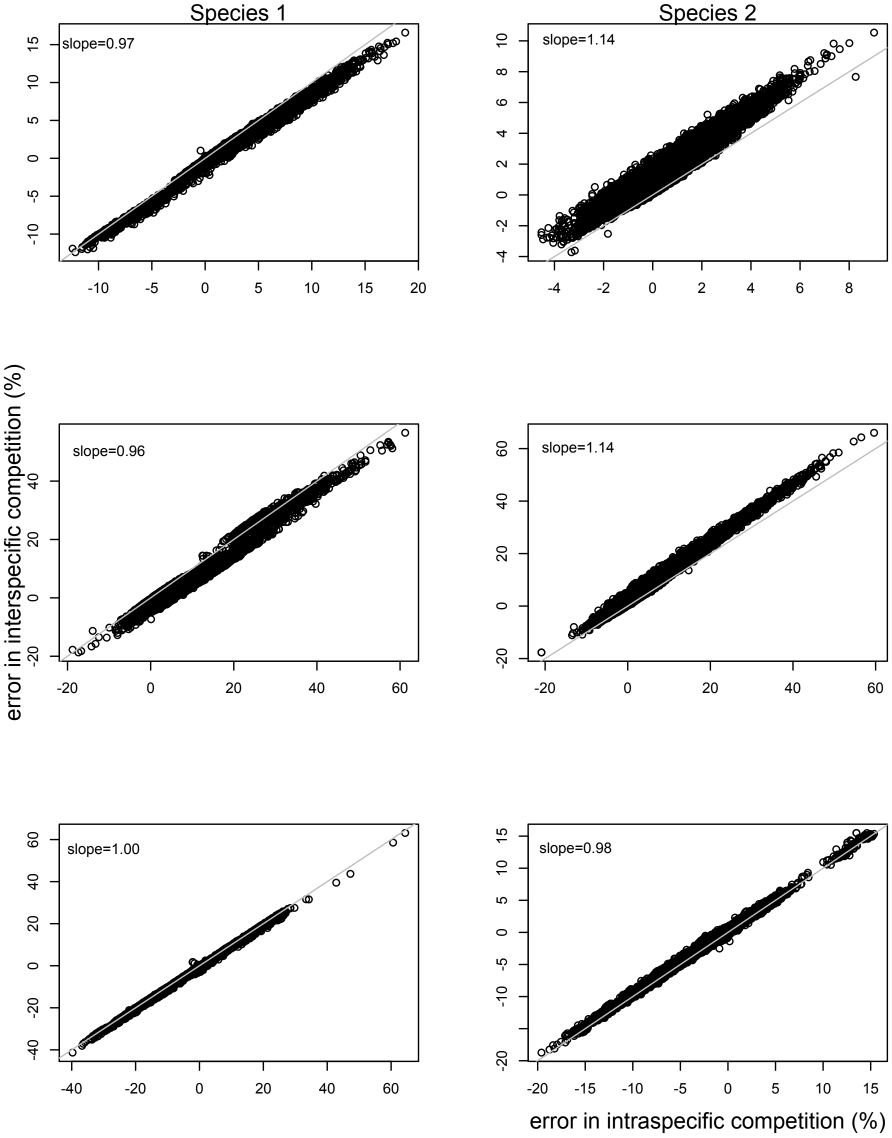

Figure S4.2. Relationship between the errors rates of intra and interspecific competition estimates. The gray line corresponds to the identity, and the reported slope was obtained from a type-II regression. The three different rows correspond to each of the three scenarios.

Response-surface experiments rapidly become prohibitive as the number of species and experimental densities increases. Another issue is that such experiments are usually conducted for short time periods (Adler et al. 2018). Observational studies such as ours solve these problems because they do not demand an extensive manipulative setup, but rely on densities and density combinations already available in nature. One issue that arises from this approach is that it is unlikely to find all the possible combinations of densities N_1 and N_2 in nature, as it happens in experimental setups. Moreover, the available combinations may be biased, leaving unpopulated large portions of the space where the response surface is to be fitted. For instance, if squares with large densities of either species are already rare, squares with large densities of *both* species would then be completely absent (compare Tables S4.2 A and B; note the large triangular region with no data in B).

Table S4.2. Data coverage in different kinds of studies. The × indicates that the combination of densities of the focal and associated species is included in the study. The most severe case of incompleteness is C, where the different densities of the focal species are observed only in the absence of the associated species, which is only present when there is one individual of the focal species.

		A: Response surface experiment										B: Observational study										C: Extreme case								
		Focal species density →																												
		1	2	3	4	5	6	7	8	9		1	2	3	4	5	6	7	8	9		1	2	3	4	5	6	7	8	9
↓ Associated species	0	×	×	×	×	×	×	×	×	×	0	×	×	×	×	×	×	×			0	×	×	×	×	×	×	×	×	×
	1	×	×	×	×	×	×	×	×	×	1	×	×	×			×			×	1	×								
	2	×	×	×	×	×	×	×	×	×	2	×	×	×	×	×					2	×								
	3	×	×	×	×	×	×	×	×	×	3	×	×		×						3	×								
	4	×	×	×	×	×	×	×	×	×	4	×	×	×							4	×								
	5	×	×	×	×	×	×	×	×	×	5	×	×		×						5	×								
	6	×	×	×	×	×	×	×	×	×	6	×		×							6	×								
	7	×	×	×	×	×	×	×	×	×	7	×	×								7	×								
	8	×	×	×	×	×	×	×	×	×	8		×								8	×								
	9	×	×	×	×	×	×	×	×	×	9	×									9	×								

The accurate estimation of interaction strengths may depend on having a good representation of the combinations of N_1 and N_2, especially if non-linear models are being fitted (Goldberg and Scheiner 2001). To avoid this problem we visually inspected our data by preparing, for every species pair, a table such as Table S4.2. When there were few co-occurences of a species pair or there where few combinations of densities, we decided *a priori* not to estimate the respective interaction coefficient.

The remaining species had a better coverage of the combinations of densities. As an indicator of this, we can use, for every pair of species *i* and *j,* the coverage index $c_{i,j}$

$$c_{i,j} = \frac{M_{i,j}}{N_i^{(90)} N_j^{(90)}} \qquad \text{(Eq. S4.3)}$$

where $N^{(90)}$ is the 9th decile of observed densities of a species, and $M_{i,j}$ is the number of combinations of densities —again, below each species' 9th decile— for which we had at least one datum. The denominator in this equation is the number of possible combinations of densities, so $c_{i,j}$ is the fraction of those combinations that were actually observed. For instance, Table S4.2 A would have a c value of 1 because all density combinations are present. Cases B and C would have values of 0.36 and 0.20, respectively. We use the 9th decile for calculations because this comprises most of the observed densities in nature, and it is the interval where it is critical to have accurate estimates of interaction strengths. Note that $c_{i,j} \neq c_{j,i}$, because, when estimating the effect of *j* on *i*, species *i* has to be present and thus $N_i > 0$; in contrast, when estimating the effect of *i* on *j,* data where $N_i = 0$ are useful. This means that $c_{i,j}$ and $c_{j,i}$ are calculated from slightly different datasets.

For all the species pairs that we included in our study $c > 0.75$, with a mean of 0.99 (Table S4.3). Nevertheless, even with a high *c* value there may be insufficient data to fit a model confidently, as most data may be concentrated in low densities. To assess the effect that this can have on our analyses we ran new simulations. Simulations consisted of 9000 squares followed for ten years using the parameters from scenario 3 of the measurement error analysis. For these simulations we set the densities at the beginning of each annual transition to those shown in the Table S4.2. In one simulation we used a complete response-surface experiment, so the initial density combinations correspond to those in Table S4.2 A. In the other simulation we used the densities from an extremely incomplete design as depicted in Table S4.2 C. This scenario is a (extreme) caricature of our data. As before, new parameters were estimated based on the three datasets by means of likelihood maximisation using package bbmle.

able S4.3. Coverage indices for species pairs. The dash indicates that the pair was not included *a priori* in the analyses ecause there were few data or the coverage was poor based on a visual assessment. Species names abbreviations are the ame shown in Appendix S6.

	aa	bc	bp	bt	cd	cs	fp	hp	mk	mp	pn	rt	sp	st	sd	se	tm	ta	tc
a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00
c	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
p	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
t	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	—	—	1.00	1.00	1.00	1.00	1.00
d	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	—	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00
s	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	—	1.00	1.00	—	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	—	1.00	—	1.00	1.00
p	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
k	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00
p	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	—	1.00	1.00	1.00	1.00
n	—	1.00	1.00	0.94	1.00	1.00	—	—	1.00	0.76	1.00	0.96	—	—	—	1.00	1.00	1.00	0.98
	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00
	1.00	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	—	1.00	—	1.00	1.00
d	—	—	—	1.00	1.00	1.00	—	1.00	1.00	—	1.00	1.00	—	—	1.00	1.00	1.00	1.00	1.00
	0.96	1.00	1.00	1.00	1.00	0.94	0.88	1.00	1.00	0.88	1.00	0.94	0.78	0.84	—	1.00	1.00	1.00	0.94
n	—	1.00	—	1.00	1.00	1.00	0.81	0.97	1.00	—	1.00	0.97	0.81	—	0.75	1.00	1.00	—	0.83
	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	0.96	1.00	0.80	1.00	1.00	1.00	1.00
	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00	—	1.00	1.00	1.00	1.00

The results from the two analyses are virtually identical. The difference between the parameters used to generate the data and the estimates ($|e_\beta|$) was 0.0094 on average in both cases, i.e., < 1%. Moreover, the confidence intervals for the parameters were smaller in the case were sampling was concentrated in low-density squares (as in Table S4.2 C). The ratio of the standard error to parameter estimates in that scenario was 0.04, whereas the ratio was 0.12 for the data where all possible density combinations were equally sampled (as in Table S4.2 A).

These results indicate that even with a poor coverage of density combinations the estimates are reliable. This is perhaps not so surprising. In equation S4.1 the densities N_i

and N_j are combined in a linear fashion to determine competition. The effect of species j over species i does not depend on the density of i, so it is relatively irrelevant whether species are observed in different combinations.

Random effects

Spatial variability may affect population dynamics. Given our sampling design, in which 0.1 × 0.1 m squares are grouped in 1 m^2 quadrats, it is likely that squares in a quadrat are not independent and have similar behaviors. This problem would usually tackled by incorporating quadrat as a random effect. However, we decided to drop the random effects for the following reasons: The model is non-linear, which makes it already quite difficult to estimate random effects. It also has an unfriendly error structure (negative binomial error), and has a very large number of parameters to be estimated. Moreover, parameters are correlated, compromising the identifiability of the model. This means that it is easy for parameter estimates to be far from the optimum, because many combinations of parameters give similar likelihoods. It seemed likely that the error caused by increased unidentifiability would be much larger than that induced by omitting the random effects. Finally, we need to consider the movement of seeds between quadrats to avoid biases. This implies an extremely complicated function from the viewpoint of derivatives, making it difficult for optimization processes to find a maximum. During our first attempts at fitting we dropped a large number of species that we intended to analyze to simplify the problem, and we believe that now we are currently near the limit of complexity that we can incorporate given the information that we have. Given the fact that relative nonlinearity is thought to increase with species numbers, we believe that keeping a "large" number (19) of species in our analysis is critical for our goals. Thus, it was impossible to use mixed effects during fitting.

However, if there are small differences in the conditions between quadrats, or the intra-quadrat variability is very large, then quadrat membership would not contribute much to determining the dynamics in any given square. To assess the effects of quadrats used a simplified version of the Hassell model that we used to describe population dynamics. By setting ω to one, as it happens in most plants species (Freckleton and Watkinson 2002), the Hassell model becomes the Beverton-Holt equation:

$$N_{t+1} = \frac{\lambda N_t}{1+\alpha N_t} \qquad \text{(Eq. S4.4)}$$

which can be linearized as

$$\frac{N_t}{N_{t+1}} = \frac{\alpha}{\lambda} + \frac{1}{\lambda} N_t = \beta_0 + \beta_1 N_t \qquad \text{(Eq. S4.5)}$$

It is now easy to incorporate a random effect. We would expect that the population growth rate changes between years, but also among quadrats. Using the parameterization with betas in the last equation, $\lambda=1/\beta_0$, we added the year and the quadrat as random effects on the intercept of the model. We used the glmer function of lme4 package in R (Douglas et al. 2015) with a Gaussian error function and an inverse link. We found that, for most of the species, the contribution of the quadrats to differences λ (measured as the fraction of the variation in growth rates explained by the quadrat identity with respect to the sum of the residual variation plus the variation between quadrats) was less than 0.2 (Figure S4.3). This suggests that, after accounting for intraspecific competition and annual variability, quadrats make a relatively small (< 20%) contribution to the variations in population dynamics. Therefore, we deem it unlikely that the inclusion of a random effect would have a large effect on our estimates.

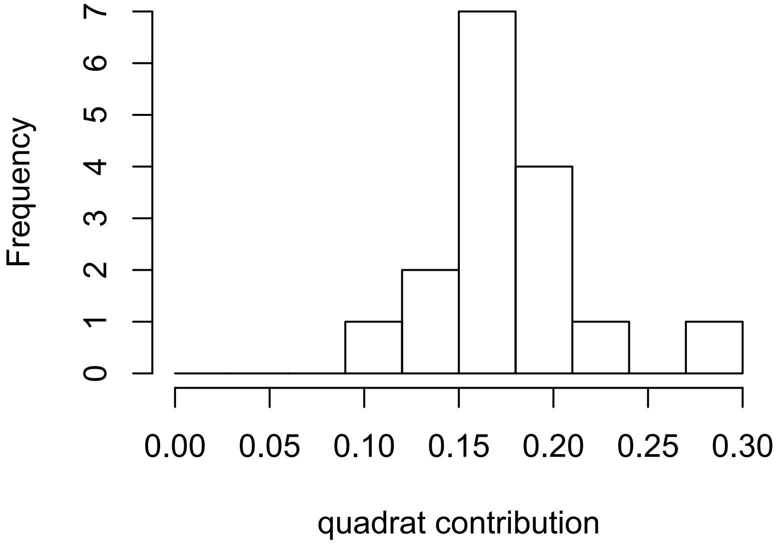

Figure S4.3. Frequency distribution of the proportion variability explained by quadrat identity.

Likelihood penalization

When fitting our population dynamics models, we penalized the log-likelihood because omega values far from 1 seem to be biologically unlikely (Freckleton and Watkinson 2001); see Appendix S3). Here we assess if the penalty produces a bias the contribution of different coexistence mechanisms to the long-term low-density population growth rate. To do this, we used the parameters of scenario 3, with the sole exception of *b* values. With those parameters, we simulated abundance data for ten years in 10,000 squares. We conducted ten simulations, using a different *b* value in each one where, for species 1, $b \in \{0.1, 0.2, 0.3, \dots, 1.0\}$, and for species 2 $b \in \{0.2, 0.3, 0.4, \dots, 1.1\}$ (the value for the second species was always 0.1 units above species 1, as it happens in the original parameters of scenario 3). We focused on *b* values because they determine the storage effect (see Appendix S1), and also determine the magnitude of the penalty. We used the artificial data series to fit equation 1 with and without the likelihood penalty using the mle2 function of bbmle package in R with negative binomial error.

Once the parameters had been fitted, we estimated $\Delta\hat{I}$, $\Delta\hat{N}$ and $r_i' = \Delta\mathscr{E} - \mathscr{C}^{\{-i\}*}$ following the procedures detailed in Appendix S5. The differences between the estimates obtained with the penalty (with a *p* subscript) with respect to the unpenalized estimates were small (Table S4.4). This was the case even when the penalty was very large, forcing ω to be close to one. However, when the relative differences were considered instead of the absolute ones, larger differences in the estimates with and without penalty were observed. As expected, when ω was close to one, and the penalty was small (as expected from empirical observations (Freckleton and Watkinson 2001), the penalty had a very small effect on our estimates. This was not the case when large penalties were imposed (Table S4.4). It is important to note that the differences between the fitted parameters between both procedures were small over a large range of penalties (Table S4.4). If we recall that, in the phase two of the fitting procedure we removed the penalty and allowed all parameters to change by up to ± 30 % of their values estimated in phase one, we would expect that parameters with and without the penalty would become identical (more specifically, this would be the case if the last column in table S4.4 reports a value smaller than 0.3). Under such scenario the differences between the penalized and unpenalized estimates of coexistence mechanisms would be zero. Finally, it must be noted that positive and negative differences between both procedures were observed, son no systematic bias can be detected.

Table S4.4. Differences between the contributions of the different coexistence mechanism obtained from parameters fitted without and with penalization. The relative differences, i.e., the differences divided by the unpenalized estimate of the parameter, are reported in parenthesis. The value of the penalty and the mean fitted ω parameter are also reported, as well as the maximum relative difference observed between the parameters fitted by the two procedures. If this difference is smaller that 0.3, the removal of the penalty in phase two of the fitting procedure would erase the differences between both procedures.

Focal species	Penalty	ω	$r_{ip}' - r_i'$	$\Delta\hat{I}_p - \Delta\hat{I}$	$\Delta\hat{N}_p - \Delta\hat{N}$	Maximum relative differerence in parameters
1	90438.14	0.5956	0.00104 (0.01251)	-0.00040 (-0.1649)	-0.00085 (-0.3261)	3.001
1	1019.072	0.6608	-0.00490 (-0.05519)	0.00244 (0.8421)	0.00160 (0.4649)	2.578
1	20.3794	0.7025	-0.00221 (-0.02136)	0.00079 (0.1347)	0.00034 (0.0531)	1.469
1	0.6397	0.7443	-0.00407 (-0.03346)	0.00125 (0.1253)	0.00143 (0.1435)	0.733
1	0.0301	0.7800	-0.00248 (-0.01879)	0.00069 (0.0649)	0.00076 (0.0712)	0.237
1	0.0021	0.8576	0.00006 (0.00045)	-0.00012 (-0.0078)	-0.00008 (-0.0050)	0.033
1	0.0002	0.9366	-0.00024 (-0.00170)	0.00024 (0.0137)	0.00034 (0.0190)	0.003
1	0.0037	0.9980	-0.00530 (-0.03590)	0.00456 (0.2625)	0.00497 (0.2904)	0.032
1	5.4616	0.9901	0.00541 (0.03009)	0.00345 (0.1804)	0.00336 (0.1752)	0.736
1	75784.67	0.9905	0.02940 (0.12782)	-0.00153 (-0.14949)	-0.00192 (-0.1883)	2.497
2	2038.573	0.6077	-0.01732 (-0.03298)	0.00058 (-0.2336)	0.00014 (-0.0672)	0.843
2	68.3969	0.7010	-0.00688 (-0.01214)	-0.00440 (-13.4118)	-0.00447 (-14.2303)	0.501
2	3.1196	0.7747	-0.01451 (-0.02387)	-0.00198 (-2.7448)	-0.00151 (-2.0179)	0.369
2	0.1881	0.8569	-0.00648 (-0.01009)	-0.00351 (-1.2110)	-0.00335 (-1.0993)	0.190
2	0.0149	0.9614	-0.00094 (-0.00137)	-0.00166 (-0.2265)	-0.00147 (-0.2002)	0.059
2	0.0016	1.0286	-0.00125 (-0.00175)	-0.00009 (-0.0101)	0.00032 (0.0388)	0.014
2	0.0034	1.1250	0.00194 (0.00261)	-0.00008 (-0.0063)	0.00009 (0.0079)	0.034
2	4.3901	1.1443	0.02507 (0.03320)	-0.00192 (-0.1217)	-0.00193 (-0.1215)	0.731
2	61775.4	1.1577	0.04667 (0.06044)	0.00460 (0.2472)	0.00455 (0.2443)	37.337

Seed survival

Because most of the species in the study site are annuals, seed survival may have an important effect on plant-plant interactions as well as population dynamics. Particularly in annual plant populations, adults could come from seeds produced during any reproductive event. These means that adult emergence in a single season represents the integration of competition across every one of these annual seasons, which may bias our competition estimations. However, if seed survival is low, we could expect that the adult emergence in a single season represents appropriately the competition experienced in the previous year.

A burial experiment was set up to determine seed survival after six and 18, and 30 months. Seeds were collected in two different dates: November 2013 and November 2014. Collected seeds were divided into samples of 25-50 seeds. They were contained in organza mesh bags and were buried at two cm depth. As we observed that most of the seeds remained in the soil surface and that they do not get buried frequently, we also conducted a seed survival experiment without burial. Six samples of 25 seeds from each study species were set on the soil surface during six months. This interval of time corresponds to the time between the seed dispersal season to the establishment season. After that time, we recovered the seed samples and we evaluated seed survival by two germination trials. Ungerminated seeds were cut or poked through the seed coat. Seeds with juicy, oily, or fleshy embryos were regarded as viable.

Assuming that 25 % of the seeds get buried (a seemingly large figure), we estimate the probability that a seed remains viable in the seed bank after 18 months of being released (P_{S2}) as:

$$P_{S2} = P_{buried} + P_{surface} \qquad \text{(Eq. S4.6)}$$

$$P_{buried} = 0.25 P_{18b}$$
$$P_{surface} = 0.75\, P_{6s}\, (P_{18b} / P_{6b})$$

where P_{buried} is the seed survival probability after being buried for two growing seasons. $P_{surface}$ is the probability of a seed survives the first growing season in the soil surface and then the second growing season in the soil seed bank. P_{18b} is the seed survival probability after being buried for 18 months. P_{6s} is the seed survival probability after six months on the soil surface and P_{6b} is the seed survival probability after six months buried.

The average seed survival to the second germination period was 0.19 (Fig. S4.4). Survival to the third one was on average reduced to 1/3 of the previous figure, suggesting that seed banks are relatively short lived. Note that these probabilities are only considering the potential of a seed to survive to the second germination season. However, seed banks in natural conditions are also affected by predation, reducing the seed survival probabilities even more. This evidence suggests that is unlikely that seed survival biased our competition estimates in a critical way for most of our species. Please see Appendix S1 for further evidence that seed banks do not affect our estimates of competition and population growth rate in any way that may affect the estimations of coexistence-mechanism estimations.

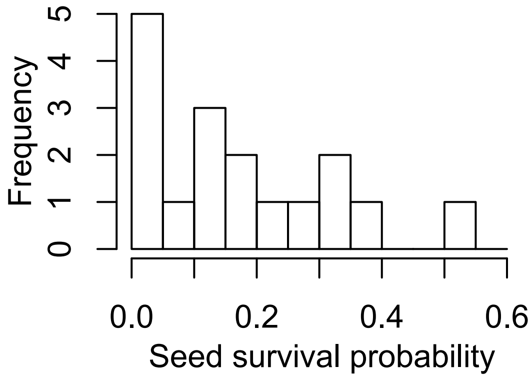

Figure S4.4 Frequency distribution of seed survival probabilities to the second germination season.

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Appendix S5. Model development and analysis

POPOULATION GROWTH MODEL

A large number of studies have found that the best function to describe population growth in plants is the Hassell model (Freckleton and Watkinson 2001) :

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1+\sum_{l=1}^{s}\alpha_{jl}N_l\right)^{\omega_j}} \quad , \qquad \text{(Eq. S1)}$$

where $N_{j,t}$ is the number of individuals in the population of species j at time t, $\lambda_{j,t}$, is the intrinsic growth rate (*i.e.*, in the absence of competition) of the population at time t, α_{jl} is the per-capita competition effect of species l on species j, ω_j is a constant, and s is the number of species in the community. We will use the subindex j to denote that a parameter corresponds to the j^{th} species. To deal with temporal fluctuations, the easiest way to calculate the long-term growth rate of the population is to work on the log scale, *i.e.*,

$$r_{j,t} = \ln\frac{N_{j,t+1}}{N_{j,t}} = \ln\lambda_{j,t} - \omega_j \ln\left(1+\sum_{l}\alpha_{jl}N_l\right) , \qquad \text{(Eq. S2)}$$

where $r_{j,t}$ is the growth rate of the species at time t.

Chesson's (1994) theory of coexistence in fluctuating environments requires that we redefine this expression in terms of environmental and competition parameters, represented by $E_{j,t}$ and $C_{j,t}$, respectively. From previous work (Martorell and Freckleton 2014), there is strong evidence that the intrinsic growth rate λ is heavily dependent on annual environmental conditions, hence

$$E_{j,t} = \ln\lambda_{j,t} . \qquad \text{(Eq. S3)}$$

Because the last term in Eq. S2 comprises the competition experienced by species j, we define

$$C_{j,t} = \ln\left(1+\sum_{l}\alpha_{jl}N_l\right) \quad , \qquad \text{(Eq. S4)}$$

so we can rewrite Eq. S2 as

$$r_{j,t} = E_{j,t} - \omega_j C_{j,t} \quad . \qquad \text{(Eq. S5)}$$

For simplicity of notation we will omit t from $E_{j,t}$ and $C_{j,t}$ in the remainder of the text.

One of the mechanisms that has been proposed for coexistence promoted by environmental fluctuations is the storage effect. For it to occur, the relationship between E_j

and C_j needs to be non-additive (Chesson 1994, 2000). Non-additivity arises naturally in many demographic models, such as those of plants with seed banks or perennial individuals. In our study we have annuals and perennials, and species whose seed banks differ in terms of size and longevity (V. Zepeda, unpublished data). There are population models that explicitly include longevity and seed bank dynamics in addition to competition terms such as those in Eq. S2. However, model fitting for non-linear, highly dimensional models Eq. S2 already requires λ-values, one per study year, plus 19 α_{lj} and one ω_j = 32 parameters) is challenging, so we opted for a simple, "generic" function where non-additivity can occur regardless of the underlying mechanisms that promote it. Noting that ω_j may reflect seed bank dynamics or perenniality, which, in most studies on storage effects (Pake and Venable 1995, 1996, Adondakis and Venable 2004, Facelli et al. 2005, Adler et al. 2006, Adler et al. 2009) change over time (See Appendix S1), we define

$$\omega_j = e^{a_j + b_j E_j} \quad . \qquad \text{(Eq. S6)}$$

The exponential is required to keep ω_j positive. Otherwise, the competition parameter would become a facilitation term, violating the assumption that the relationship between r_j and C_j is monotonically decreasing (Chesson 1994). A positive value of b_j implies that competition is stronger in favorable years, something that can happen for instance if plants in the neighborhood grow larger. Thus, on a log scale, the model for the population growth of species j is

$$r_j = E_j - e^{a+bE_j} C_j \, . \qquad \text{(Eq. S7)}$$

STANDARIZATION

To analyze how different mechanisms contribute to species coexistence we follow Chesson (1994), and we will use square brackets to make reference to equation numbers in that paper. Chesson's model is based on a Taylor series approximation around a given reference value E^*_j, accuracy depends on the actual E_j values fluctuating closely around it. In Eq. S7, a natural choice[1] is $E^*_j = \bar{E}_j$, the mean value of E_j. The respective equilibrial value for

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[1] Another quite natural choice would be to set E^*_j to the average of the log-λ values of all species. This alternative would not result in necessarily low $\Delta \mathscr{E}_i$ values (Note that in Eq. S3 $\Delta \mathscr{E}_i$ needs to be small whenever the means of $\mathscr{E}$ tend to be small, an inevitable result of our choice that $E^*_j = \bar{E}_j$. See discussion in the main text), making it attractive if we are interested in estimating the contribution of equalizing mechanisms to coexistence. However, this option results in larger differences between the reference value E^*_j and annual E_j values. Apparently this violates the assumption of small variations: the estimated growth rates for a few species using the quadratic approximation were quite different from the ones estimated from Eq. S7, which is the model that we are trying to approximate. In contrast, when $E^*_j = \bar{E}_j$, the reference value is closer to the annual values, and the approximation was very accurate (see results in the main text).

competition, i.e., the amount of competition needed for $r_j = 0$ given that the environmentally dependent parameter $E_j = E_j^*$ is

$$C_j^* = \frac{\bar{E}_j}{e^{a_j+b_j\bar{E}_j}} . \tag{Eq. S8}$$

The environmental and competition parameters in the model need to be standardized around the equilibrial values chosen. From [6] and [7], the standard environmentally-dependent and competition parameters, $\mathscr{E}_j$ and $\mathscr{C}_j$, are

$$\begin{aligned} \mathscr{E}_j &= E_j - e^{a_j+b_jE_j}\frac{\bar{E}_j}{e^{a_j+b_j\bar{E}_j}} \\ \mathscr{E}_j &= E_j - e^{b_j\left(E_j-\bar{E}_j\right)}\bar{E}_j \end{aligned} , \tag{Eq. S9}$$

and

$$\mathscr{C}_j = e^{a_j+b_j\bar{E}_j}C_j - \bar{E}_j . \tag{Eq. S10}$$

To estimate the variances and covariances of $\mathscr{E}_j$ and $\mathscr{C}_j$ we need the first-order Taylor series approximation [8,9]:

$$\mathscr{E}_j \approx \left(1 - b_j\bar{E}_j\right)\left(E_j - \bar{E}_j\right) \tag{Eq. S11}$$

and

$$\mathscr{C}_j \approx e^{a_j+b_j\bar{E}_j}\left(C_j - C_j^*\right) \tag{Eq. S12}$$

However, to estimate the means of $\mathscr{E}_j$ and $\mathscr{C}_j$, we must add the second-order terms in the Taylor series, so:

$$\mathscr{E}_j \approx \left(1 - b_j\bar{E}_j\right)\left(E_j - \bar{E}_j\right) - \frac{b_j^2\bar{E}_j}{2}\left(E_j - \bar{E}_j\right)^2 \tag{Eq. S13}$$

(note that C_j remains as in Eq. S12). We now need to put Eq. S7 in terms of the standard parameters. For this we require a final parameter γ_j [14]:

$$\gamma_j = \left.\frac{\partial^2 r_j}{\partial \mathscr{E}_j \partial \mathscr{C}_j}\right|_{0,0} .$$

Considering that the derivative of a function $f(x)$ with respect to another function $g(x)$ of same variable x is $(\partial f(x)/\partial x) / (\partial g(x)/\partial x)$, and that $\mathscr{E}_j$ and r_j share just a common variable E_j, then

$$\gamma_j = \frac{\partial}{\partial \mathscr{C}_j}\left(\frac{\dfrac{\partial r_j}{\partial E_j}}{\dfrac{\partial \mathscr{E}_j}{\partial E_j}} \right)\Bigg|_{0,0} = \frac{\partial}{\partial \mathscr{C}_j}\left(\frac{\dfrac{\partial E_j - e^{a_j+b_jE_j}C_j}{\partial E_j}}{\dfrac{\partial\left(1-b_j\bar{E}_j\right)\left(E_j-\bar{E}_j\right)}{\partial E_j}} \right)\Bigg|_{0,0} = \frac{\partial}{\partial \mathscr{C}_j}\left(\frac{1-b_je^{a_j+b_jE_j}C_j}{1-b_j\bar{E}_j} \right)\Bigg|_{0,0} .$$

Now, bearing in mind that $\mathscr{C}_j$ and C_j share only population sizes N, and letting $D = \partial C_j / \partial N$,

$$\gamma_j = \frac{\partial \dfrac{1-b_je^{a_j+b_jE_j}C_j}{1-b_j\bar{E}_j}}{\partial \mathscr{C}_j}\Bigg|_{0,0} = \frac{\dfrac{\partial \dfrac{1-b_je^{a_j+b_jE_j}C_j}{1-b_j\bar{E}_j}}{\partial N}}{\dfrac{\partial e^{a_j+b_j\bar{E}_j}C_j-\bar{E}_j}{\partial N}}\Bigg|_{0,0} = \frac{\dfrac{b_je^{a_j+b_jE_j}}{b_j\bar{E}_j-1}D}{e^{a_j+b_j\bar{E}_j}D}\Bigg|_{0,0} = \frac{b_je^{a_j+b_jE_j}}{\left(b_j\bar{E}_j-1\right)e^{a_j+b_j\bar{E}_j}}\Bigg|_{0,0} .$$

Simplifying and evaluating at $\mathscr{E}_j = 0$, which happens when $E_j = \bar{E}_j$,

$$\gamma_j = \frac{b_je^{b_jE_j}}{\left(b_j\bar{E}_j-1\right)e^{b_j\bar{E}_j}}\Bigg|_{0,0} = \frac{b_j}{\left(b_j\bar{E}_j-1\right)} \qquad \text{(Eq. S14)}$$

Using the approximations in Eq. S12 and Eq. S13, the standardized quadratic approximation to Eq. S7 is [13]:

$$r_j \approx \mathscr{E}_j - \mathscr{C}_j + \gamma_j\mathscr{E}_j\mathscr{C}_j = \mathscr{E}_j - \mathscr{C}_j + \frac{b_j}{\left(b_j\bar{E}_j-1\right)e^{b_j\bar{E}_j}}\mathscr{E}_j\mathscr{C}_j \qquad \text{(Eq. S15)}$$

For subadditivity (one of the ingredients of the storage effect) to occur, γ_j should be negative (Chesson 1994), which occurs only if $0 < b_j < 1/\bar{E}_j$ (note that $\bar{E}_j$ must be positive for any species to persist in a system, and thus negative values of $\bar{E}_j$ are of no biological interest). The quadratic approximation in Eq. S15 is the basis for the subsequent analyses.

ANALYSIS OF THE MODEL

Most of modern coexistence theory is based on the invasibility concept (Siepielski and McPeek 2010, HilleRisLambers et al. 2012). If a population (the invader) tends to grow when its numbers are low and the rest of the species (the residents) are in their equilibrium, then the invader cannot go extinct and it can invade the community. If all the species in the community have this property, i.e., there is mutual invasibility, then coexistence is stable (Chesson 1994, 2000). Mutual invasibility occurs if the long-term low-density growth rate, $\bar{r}_i$, of each species is positive. The value of $\bar{r}_i$ is simply the average of the r values over time setting the density of the species to zero and letting the remainder of the community to reach its stationary state. Because under such conditions the species is an invader in the community, we will use the subindex i for it. The remainder species are known as residents, and thus are referred to by the subindex r.

To perform the analysis, we need the densities of the resident species at the equilibrium in the absence of the invader, $N_r^{\{-i\}*}$ (the superindex $\{-i\}$ will indicate that the invader is absent throughout the text). Because at the equilibrium the growth rates are zero:

$$e^{a_r+b_r\bar{E}_r}\ln\left(1+\sum_{l\neq i}\alpha_{rl}N_l^{\{-i\}*}\right)-\bar{E}_r=0\,. \qquad \text{(Eq. S16)}$$

That is, we need the equilibrial densities of the residents at which competition balances their environmental effects. Let p be the number of resident species ($p = s - 1$). To estimate $N_r^{\{-i\}*}$, we first rewrite Eq. S16 for all residents as

$$\begin{bmatrix} e^{\left(\frac{\bar{E}_1}{e^{a_1+b_1\bar{E}_1}}\right)}-1 \\ \vdots \\ e^{\left(\frac{\bar{E}_p}{e^{a_p+b_p\bar{E}_p}}\right)}-1 \end{bmatrix} = \begin{bmatrix} \alpha_{11} & \cdots & \alpha_{1p} \\ \vdots & \ddots & \vdots \\ \alpha_{p1} & \cdots & \alpha_{pp} \end{bmatrix} \begin{bmatrix} N_1^{\{-i\}*} \\ \vdots \\ N_p^{\{-i\}*} \end{bmatrix}, \qquad \text{(Eq. S17)}$$

so

$$\mathbf{N}^{\{-i\}*} = \begin{bmatrix} N_1^{\{-i\}*} \\ \vdots \\ N_p^{\{-i\}*} \end{bmatrix} = \begin{bmatrix} \alpha_{11} & \cdots & \alpha_{1p} \\ \vdots & \ddots & \vdots \\ \alpha_{p1} & \cdots & \alpha_{pp} \end{bmatrix}^{-1} \begin{bmatrix} e^{\left(\frac{\bar{E}_1}{e^{a_1+b_1\bar{E}_1}}\right)}-1 \\ \vdots \\ e^{\left(\frac{\bar{E}_p}{e^{a_p+b_p\bar{E}_p}}\right)}-1 \end{bmatrix}, \qquad \text{(Eq. S18)}$$

where the matrix inverse is represented by -1. In some resident-invader scenarios, a few $N_r^{\{-i\}*}$ were negative, corresponding to species that become extinct from the resident communities. In those cases, the extinct species were removed from the invasibility analyses (equivalent to setting $N_r^{\{-i\}*} = 0$). This procedure had a negligible effect on our estimations and is biologically more sensible.

With these data we can partition $\bar{r}_i$ into the contributions of the different coexistence mechanisms. For this purpose, a useful expression for $\bar{r}_i$ is [19]:

$$\bar{r}_i = \Delta\mathcal{E}_i - \Delta\mathcal{C}_i + \Delta I_i\,, \qquad \text{(Eq. S19)}$$

$\Delta\mathcal{E}_i$ is a measure of fitness (*sensu* Chesson 2000) differences. If this value is positive, the invader has an advantage over the residents due to its larger growth rate. If it is zero or close to zero, the fitness disadvantage is small, leading to very long times to competitive exclusion, and thus to extended, but unstable, coexistence. Thus, small $\Delta\mathcal{E}_i$ values correspond to strong equalizing mechanisms. Without additional stabilizing mechanisms, species with negative $\Delta\mathcal{E}_i$ may become extinct from the community. $\Delta\mathcal{C}_i$ is a measure of the difference between intra and interspecific coexistence (plus relative non-linearity, see below). If intraspecific interactions are stronger (as it may happen if there is niche differentiation), $\Delta\mathcal{C}_i$ will be positive, allowing species to overcome their fitness disadvantages and leading to stable coexistence. Importantly, ΔI_i is the storage effect. $\Delta\mathscr{C}_i$ and ΔI_i correspond to stabilizing coexistence mechanisms (Chesson 1994, 2000).

All these Δ values are weighted comparisons between the residents and the invader [20–22]:

$$\Delta\mathscr{E}_i = \mathrm{E}\,\mathscr{E}_i - \sum_r q_{ir}\,\mathrm{E}\,\mathscr{E}_r\,, \qquad \text{(Eq. S20)}$$

$$\Delta\mathscr{C}_i = \mathrm{E}\,\mathscr{C}_i^{\{-i\}} - \sum_r q_{ir}\,\mathrm{E}\,\mathscr{C}_r^{\{-i\}}\;, \text{ and} \qquad \text{(Eq. S21)}$$

$$\Delta I_i = \gamma_i\,\mathrm{E}\,\mathscr{E}_i\mathscr{C}_i^{\{-i\}} - \sum_r q_{ir}\gamma_r\,\mathrm{E}\,\mathscr{E}_r\mathscr{C}_r^{\{-i\}}\,, \qquad \text{(Eq. S22)}$$

where $\mathscr{C}_l^{\{-i\}}$ is the competition experienced by species l in the absence of the invader, and E is the mathematical expectation. To calculate the weights q_{ir}, it must be noted that the resident-species densities are limiting factors for the invaders, and thus we included them as such in Chesson's framework. By doing so, we can define $\phi_{jl}^{\{-i\}}$ as [41, 49]

$$\phi_{jr}^{\{-i\}} = \left.\frac{\partial\mathscr{C}_j}{\partial N_r}\right|_{\mathbf{N}^{\{-i\}*}} = e^{a_j+b_j\bar{E}_j}\,\frac{\alpha_{jr}}{1+\sum\limits_{l\neq i}^{p}\alpha_{jl}N_l^{\{-i\}*}}\,, \qquad \text{(Eq. S23)}$$

the $1 \times p$ vector $\boldsymbol{\phi}_i$ as

$$\boldsymbol{\phi}_i = \left\{\phi_{ir}^{\{-i\}}\right\}, \qquad \text{(Eq. S24)}$$

and the $p \times p$ matrix $\boldsymbol{\Phi}^{-i}$ as

$$\boldsymbol{\Phi}^{\{-i\}} = \left\{\phi_{mn}^{\{-i\}}\,\forall m,n \in \{1,2,\ldots,p\}\right\}. \qquad \text{(Eq. S25)}$$

Finally, the vector containing the q_{ir} values for Eqs. S5.20-S5.21 can then be calculated as [34]

$$\mathbf{q}_i = \boldsymbol{\phi}_i\left(\boldsymbol{\Phi}^{\{-i\}}\right)^{-1}\;. \qquad \text{(Eq. S26)}$$

At this point, it is important to note that the precise values of $\Delta\mathscr{E}_i$ and $\Delta\mathscr{C}_i$ in Eq. S19 are dependent on the somewhat arbitrary election of E^*. Furthermore, the term $\Delta\mathscr{C}_i$ reflects both niche differentiation and relative nonlinearity. A more satisfactory way to estimate $\Delta\mathscr{E}_i$, $\Delta\mathscr{C}_i$, and ΔI_i requires the estimation of a new matrix $\boldsymbol{\Psi}$ [44]

$$\boldsymbol{\Psi}_i = \frac{1}{2}\left(\boldsymbol{\Phi}_i^{(2)} - \sum_r q_{ir}\boldsymbol{\Phi}_r^{(2)}\right), \qquad \text{(Eq. S27)}$$

which in turn depends on the matrices $\boldsymbol{\Phi}_j^{(2)}$, whose l^{th} row and m^{th} column element is [42]

$$\phi^{(2)}_{lm(j)} = \left.\frac{\partial^2 \mathcal{C}_j}{\partial N_l \partial N_m}\right|_{\mathbf{N}^{\{-j\}*}} = -e^{a+b\bar{E}_j} \frac{\alpha_{jl}\alpha_{jm}}{\left(1+\sum_k \alpha_{jk} N_k^{\{-j\}*}\right)^2} \,. \qquad \text{(Eq. S28)}$$

We can now estimate the contribution of relative non-linearity, ΔN_i, as [51]

$$\Delta N_i = \mathrm{trace}\left(\mathbf{\Psi}_i \mathbf{V}^{\{-i\}}\right) \qquad \text{(Eq. S29)}$$

where $\mathbf{V}^{\{-i\}}$ is the variance-covariance matrix of the population sizes of the resident species over time in the absence of the invader.

We now require some mathematical expectations whose analytical expressions are intractable. Thus, we estimated them numerically. Following Yuan and Chesson (2015), we used Eq. S15 to generate time series of population sizes setting the initial invader-species density to zero and the densities for the residents to 0.1. The system was iterated 2 × 10^6 times to allow it to reach its stationary state, and then 1 × 10^6 more times, from which statistics were obtained. $\mathbf{V}^{\{-i\}}$ was estimated from the population densities of the residents. We include environmental fluctuations by selecting randomly and with equal probabilities one out of the 12 annual transitions that we observed. The $\lambda_{j,t}$ values for that transition were used in the projection of population sizes into the next year. For each iteration we recorded $\Delta\mathcal{E}_i$ and $\Delta\mathcal{C}_i$ using the linear and quadratic approximations (Eqs. S11-S13). $\mathrm{E}\mathcal{E}_i$ and $\mathrm{E}\mathcal{C}_i$ in Eqs. S20-S21 were calculated as the mean of the quadratic approximations over time, but $\mathrm{E}\mathcal{E}_j\mathcal{C}_j^{\{-i\}}$ is a covariance, so it was calculated as the mean of the product of the linear approximations. From these data, we used Eqs. S19-21, S29 to estimate the contributions of all the coexistence mechanisms.

Model assumptions

The quadratic approximation had a poor performance in reconstructing environment-competition covariances, underestimating them strongly (Appendix 6:Table S4). This could be the result of the violation of some of the assumptions of Chesson's (1994) framework. This can occur if there are large fluctuations. To see if covariance tends to be underestimated under such scenario, we conducted some simulations for two species. In both species mean $\lambda = 2$, $\alpha_{11} = 0.5$, $\alpha_{12} = 0.25$, $\alpha_{21} = 0.125$, $\alpha_{22} = 0.25$, $a_1 = a_2 = 1$, $b_1 = 0.4$ and $b_2 = 0.5$. These parameters were chosen because they allowed for coexistence under a wide range of variations in λ. We estimated the environment-competition covariances from simulations using the original model and the quadratic approximation. In each simulation the standard deviation in λ-values was changed. In table S1 we report the ratio f the covariances obtained from both methods.

Increasing the magnitudes of environmental fluctuations (the standard deviation in λ-values) resulted in greater ratios, indicating that the quadratic approximation provides increasingly underestimated environment-competition covariances. While this may contribute to the negligible storage effects estimated by the approximation, in table S1 it can be seen that the covariances were strongly underestimated even when environmental fluctuations were very small. This suggests that large fluctuations are not the main cause of the underestimated covariances.

Table S1. Ratios of the environment-competition covariances obtained by the original model to the quadratic approximation. sp1 and sp2 are the two simulated species.

λ standard deviation	sp1	sp2
0.005	5209654	-89635
0.05	-882390	953242
0.1	1605	992283
0.15	4876	-31315
0.25	-79973	-89179
0.35	-708297	-155759
0.45	77749	564793
0.5	33710	164334
0.65	14576	-15824
0.75	-193953497	194012988
1	-15002854919	296243274
1.25	3.572×10^{20}	8.532×10^{18}
1.5	∞	-1.575×10^{29}
1.75	∞	-8.229×10^{8}
2	-2.201×10^{17}	-8.671×10^{16}
2.25	-4.517×10^{247}	7.481×10^{247}

A second assumption that can be violated in Chesson's framework is that a second-order Taylor expansion provides an accurate approximation to the population dynamics. We estimated the "remainder" or error introduced in the estimation of $\mathscr{E}$ by using first or second order expansions. The remainder was calculated as the difference in $\mathscr{E}$ estimated from Eq. S9 and Eqs. S11 and S13 evaluated at the observed E values. The maximum remainder for each species was selected. We found large remainders for the species with large b values, especially in the cases where the SE was incorrectly identified as ΔE by the quadratic approximation (Table S2).

The correlation between the remainder and b values suggests that cubic or higher-order terms are required to represent accurately the dynamics of population with strong subaditivity. This means that the quadratic approximation may fail, and may explain why the storage effect was misidentified.

Table S2. Remainders of the linear and quadratic approximations to $\mathscr{E}$. *b*-values for each species are include for comparison. Asterisk indicates species where the storage effect was incorrectly identified as ΔE by the quadratic approximation.

Species	*b*	Remainder (Linear)	Remainder (Quadratic)
aa*	0.620	0.03144	0.00473
bc	0.337	0.00014	0.00000
bp	0.478	0.00659	0.00031
bt*	0.473	0.09266	0.02476
cd	0.000	0.00000	0.00000
cs*	0.457	0.03267	0.00630
fp	0.000	0.00000	0.00000
hp	0.000	0.00000	0.00000
mk	0.723	0.01407	0.00134
mp*	0.398	0.33029	0.13138
pn	0.002	0.00000	0.00000
rt	0.000	0.00000	0.00000
sd	0.000	0.00000	0.00000
se	0.000	0.00000	0.00000
sp	0.000	0.00000	0.00000
st	0.000	0.00000	0.00000
ta	0.000	0.00000	0.00000
tc	0.204	0.00449	0.00047
tm	0.000	0.00000	0.00000

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Appendix S6. Species used in this study and parameters estimated for each of them

In this study we use 19 species that differ in their attributes. They cover a large range of life forms and cycles. Some basic data on each are shown in Table S1.

There are a few issues that we must bear in mind when addressing our results. First, our sampling unit was small. This introduces strong demographic stochasticity, and makes parameters difficult to estimate due to large unexplained variations in the data (Freckleton and Watkinson 2001). Thus, some of our parameter estimates have relatively large standard errors (Table S2). Consequently, the estimations of the different coexistence mechanism's contributions are probably not very accurate. The fact that the same mechanisms are important for different species (which were fitted independently; Fig. 2 in the main text) suggests, however, that we are not looking at a stochastic pattern that arises purely from random estimation errors. We also consider that the coexistence of 17 out of 19 species is unlikely to occur from random parameters.

Standard errors reported are estimated by ADMB from the second derivative of the likelihood function at its maximum. This procedure is fast but inaccurate, especially when the likelihood profile is asymmetric. This is certainly the case of many of our parameters, which were logged to restrict the to positive and biologically sensible values. When such parameters are very small (≈ 0) their logs become very negative, and small changes in the logged value are irrelevant as the parameter is still effectively zero. This lead to a very flat likelihood profile and inordinately large standard errors. Thus, we can be sure that very negative logged lambdas, alphas, and *b* values are zeros regardless of the magnitude of their s.e.

The precise values for the contributions of the different coexistence mechanisms are shown in table S3. These are the same data shown in figure 2 in the main text. Environment-competition covariances are also summarized in Fig. 3b in the main text, but the detailed dataset is shown in Table S4. Two sets of covariances are shown per species, one estimated for it as a resident (estimated assuming all species are residents for simplicity) and another as an invader, allowing the remaining species to attain they stationary distribution. For each of these two conditions, three covariances are shown. (1) *Covariance for the quadratic approximation*. This was estimated as explained in Appendix S5 (see details on the estimations of variances and covariances in the quadratic approximation there). (2) *Covariance in the original model*. We conducted simulations of the community dynamics using the original model (Appendix 5:Eq. S1) and recorded the λ values and the population sizes of each species for each simulated year. Using these data we estimated the values for the environmental ($E_{j,t} = \ln \lambda_{j,t}$) and competition $C_{j,t} = \ln\left(1 + \sum_{l} \alpha_{jl} N_l\right)$ parameters (Eq. S5.3 and Eq. S5.4). The simulations were conducted 4 million iterations, dropped the first 2 million, and the covariance between $E_{j,t}$ and $C_{j,t}$ was then estimated. (3) *Standardized covariance*. The values on which the previous two covariances are shown cannot be compared because the first one is based on standardized environmental and competition parameters, while the second is calculated from the unstandardized $E_{j,t}$ and $C_{j,t}$. To allow comparison, we used the same simulations as in the estimation of the covariance in the original model, but calculated $\mathscr{E}_j \approx \left(1 - b_j \bar{E}_j\right)\left(E_j - \bar{E}_j\right)$ and $\mathscr{C}_j \approx e^{a_j + b_j \bar{E}_j}\left(C_j - C_j^*\right)$, where $\bar{E}_j$ is the mean value of E_j. These are the same parameters used in the quadratic approximation, making it possible to compare the covariances from both models. In the results section main text, where there covariances are compared (i.e., where it reads “these covariances were substantially larger (on average over 50 times larger for residents, and 5 orders of magnitude larger for invaders)”, we used the standardized covariance. However, the covariances in the original model, which correspond to the “real” situation, were used for Fig. 3b.

Table S1. Code, family and life cycle of the study species.

Code	Species	Family	Life cycle
sd	*Stenandrium dulce*	Acanthaceae	perennial
fp	*Florestina pedata*	Asteraceae	annual
tm	*Tagetes micrantha*	Asteraceae	annual
ta	*Thymophylla aurantiaca*	Asteraceae	annual
sp	*Sanvitalia procumbens*	Asteraceae	annual
se	*Stevia ephemera*	Asteraceae	annual
hp	*Heterosperma pinnatum*	Asteraceae	annual
tc	*Tridax coronopifolia*	Asteraceae	annual
cs	*Cyperus seslerioides*	Cyperaceae	perennial
bt	*Bulbostylis tenuifolia*	Cyperaceae	perennial
pn	*Plantago nivea*	Plantaginaceae	perennial
bp	*Bouteloua polymorpha*	Poaceae	perennial
bc	*Bouteloua chondrosioides*	Poaceae	perennial
st	*Sporobolus tenuissimus*	Poaceae	perennial
mk	*Microchloa kunthii*	Poaceae	perennial
mp	*Muhlenbergia peruviana*	Poaceae	annual
aa	*Aristida adscensionis*	Poaceae	annual
rt	*Richardia tricocca*	Rubiaceae	perennial
cd	*Crusea diversifolia*	Rubiaceae	annual

Table S2. Estimated values of the λs for each of the 12 annual transitions, the interaction coefficients (α_{ij}) and parameters *a* and *b* of the population model (see Eq. 1 in the main text) ± S.E. See Table S1 for species names. *R^2 is the percent deviance explained by each species model. X corresponds to coefficients that could not be estimated because of the lack of data. Note that parameters λ, α_{ij} and *b* were exponentiated (i.e., they were incorporated in the procedure that estimates the likelihood with an exponent) to restrict them to positive values. Thus, the numbers reported here correspond to the parameters and S.E. in a log scale. The parameters in one column correspond to one focal species. See species name's list below.

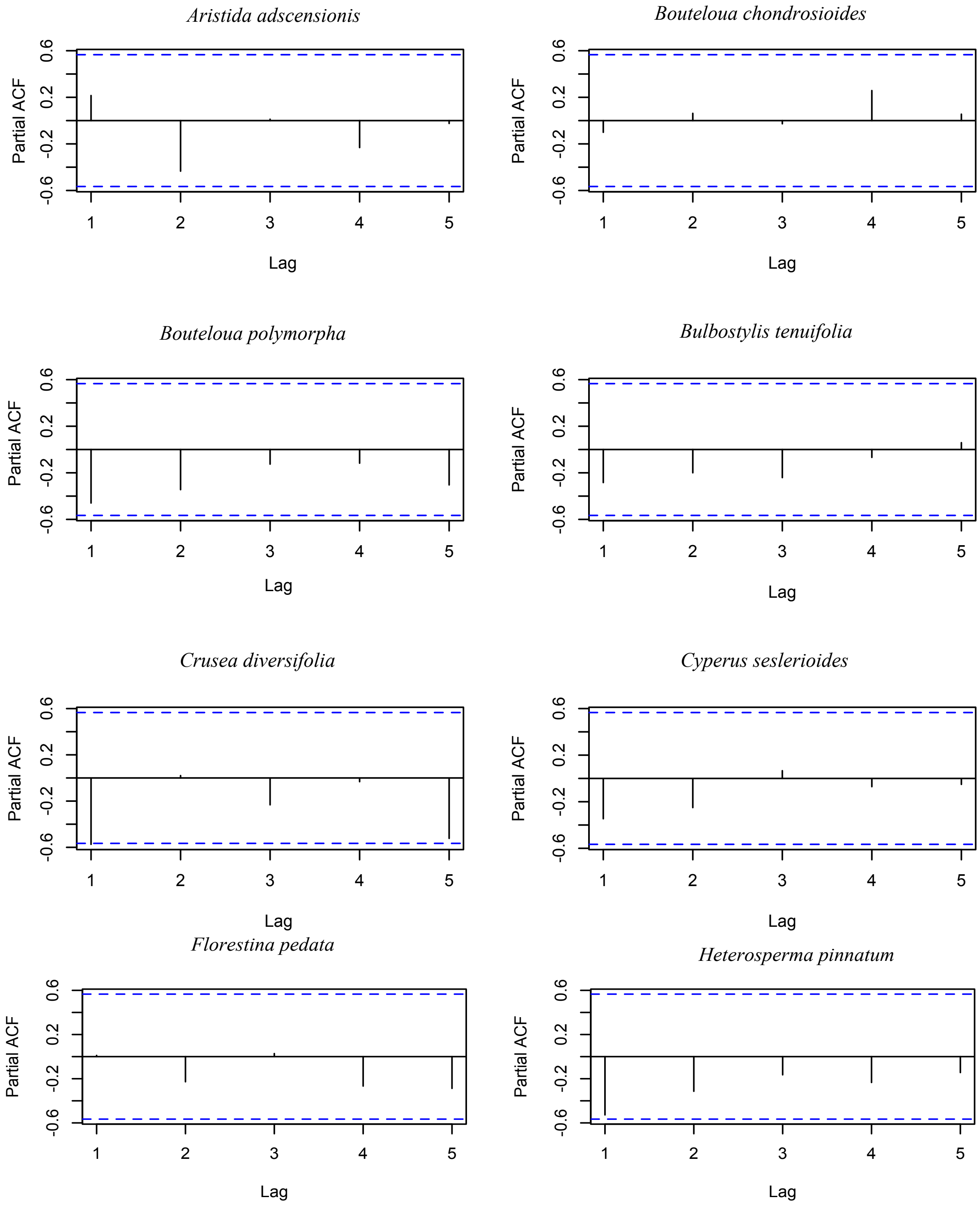
	aa	bc	bp	bt	cd	cs	fp	hp	mk	mp	pn	rt	sp	st	sd	se	tm	ta	tc
λ1	0.792 ±0.266	-0.035 ± 0.115	0.394 ± 0.007	-0.896 ± 0.358	0.491 ±0.095	0.377 ±0.154	0.331 ±0.189	0.451 ±0.151	-0.002 ± 0.009	1.691 ±0.445	-0.008 ± 0.001	0.288 ± 0.107	0.261 ± 0.191	0.349 ±0.109	0.710 ±0.203	-1.608 ± 0.264	-0.276 ± 0.131	0.739 ±0.086	0.556 ± 0.213
λ2	0.013 ±0.018	0.023 ± 0.114	0.956 ± 0.216	2.016 ±0.266	-0.084 ± 0.005	1.199 ± 0.158	-0.095 ± 0.006	0.784 ±0.159	0.643 ±0.076	1.327 ±0.338	0.234 ± 0.059	0.990 ±0.088	-0.121 ± 0.193	0.437 ±0.106	0.736 ±0.001	1.453 ±0.174	0.957 ± 0.121	0.624 ± 0.092	0.131 ± 0.001
λ3	-0.254 ± 0.220	0.037 ±0.114	0.668 ±0.170	-0.099 ± 0.135	0.432 ± 0.106	-0.671 ± 0.114	-0.955 ± 0.319	0.267 ±0.014	-0.059 ± 0.059	0.161 ±0.283	0.232 ±0.053	-0.128 ± 0.107	-0.518 ± 0.254	0.195 ±0.104	-2.000 ± 0.000	0.364 ±0.146	-0.398 ± 0.140	0.907 ± 0.076	-1.019 ± 0.16
λ4	0.119 ± 0.291	0.068 ±0.115	0.668 ± 0.170	-1.372 ± 0.208	-0.251 ± 0.122	-0.134 ± 0.141	0.357 ±0.265	-1.282 ± 0.246	0.429 ± 0.058	-0.010 ± 0.081	-0.384 ± 0.060	0.079 ± 0.108	-0.556 ± 0.249	0.325 ±0.108	0.756 ± 0.005	-0.782 ± 0.178	-0.740 ± 0.227	-0.369 ± 0.104	-0.375 ± 0.001
λ5	0.575 ±0.212	-0.057 ± 0.049	0.740 ±0.176	-0.376 ± 0.273	0.378 ±0.106	1.476 ±0.130	0.681 ± 0.261	1.537 ± 0.162	0.533 ±0.056	-2.000 ± 0.003	-0.273 ± 0.069	0.483 ±0.101	-0.101 ± 0.263	0.412 ± 0.101	0.405 ±0.216	0.813 ± 0.146	0.838 ± 0.135	-0.120 ± 0.103	1.046 ±0.307
λ6	0.052 ±0.148	0.083 ± 0.108	0.643 ±0.165	-0.243 ± 0.281	-1.114 ± 0.146	-0.905 ± 0.119	0.471 ± 0.263	-0.340 ± 0.149	0.085 ± 0.056	2.609 ± 0.156	-0.251 ± 0.074	0.115 ± 0.110	0.397 ± 0.253	-0.365 ± 0.119	0.155 ± 0.223	-0.927 ± 0.210	-1.341 ± 0.190	-0.092 ± 0.113	0.065 ±0.001
λ7	0.039 ±0.009	0.057 ± 0.106	0.566 ±0.159	1.039 ± 0.253	1.201 ±0.145	0.628 ± 0.124	0.985 ± 0.174	1.022 ± 0.128	0.138 ± 0.059	1.764 ± 0.556	1.378 ±0.063	0.691 ± 0.101	1.974 ±0.144	0.315 ± 0.124	0.563 ± 0.191	1.541 ± 0.208	1.443 ± 0.220	1.524 ± 0.111	0.726 ±0.280
λ8	0.049 ± 0.142	0.085 ± 0.081	0.766 ± 0.165	0.323 ±0.114	0.130 ± 0.002	0.146 ± 0.085	0.492 ± 0.120	0.355 ± 0.090	0.702 ± 0.046	2.128 ±0.419	0.227 ± 0.038	0.045 ± 0.001	-0.293 ± 0.195	0.317 ± 0.096	0.580 ± 0.178	0.930 ± 0.120	0.835 ± 0.075	0.177 ±0.000	-0.031 ± 0.001
λ9	-0.539 ± 0.173	0.077 ± 0.079	0.740 ± 0.162	0.607 ± 0.104	0.392 ±0.068	0.517 ± 0.094	-0.230 ± 0.139	-0.006 ± 0.001	0.195 ± 0.045	1.026 ±0.306	0.166 ± 0.039	0.525 ±0.066	0.268 ±0.008	0.522 ± 0.094	0.413 ± 0.178	0.706 ± 0.125	0.984 ± 0.072	0.380 ±0.068	0.030 ± 0.001
λ10	0.407 ± 0.127	0.022 ±0.058	0.724 ± 0.156	-0.990 ± 0.091	0.208 ±0.057	0.261 ±0.080	0.023 ± 0.005	0.846 ± 0.068	0.167 ± 0.038	-1.272 ± 0.242	-0.029 ± 0.000	-0.010 ± 0.001	0.354 ± 0.001	-0.430 ± 0.088	0.272 ±0.147	0.665 ±0.113	-0.119 ± 0.002	0.393 ±0.058	0.726 ± 0.120
λ11	1.000 ± 0.134	0.056 ± 0.071	0.647 ± 0.148	1.957 ±0.197	0.526 ± 0.059	-0.079 ± 0.076	0.970 ± 0.102	0.912 ±0.067	0.586 ±0.036	1.931 ± 0.449	0.395 ± 0.035	0.666 ± 0.054	1.138 ± 0.132	0.345 ± 0.085	0.340 ±0.132	1.419 ± 0.111	0.801 ± 0.060	1.356 ± 0.058	0.808 ± 0.126

λ12	0.648 ±0.118	0.095 ± 0.073	0.773 ±0.162	0.199 ± 0.090	-0.558 ± 0.067	-1.118 ± 0.085	-0.492 ± 0.114	-0.330 ± 0.083	0.152 ± 0.037	-0.205 ± 0.252	-0.388 ± 0.040	0.276 ± 0.057	-0.908 ± 0.175	0.145 ± 0.000	-0.005 ± 0.004	-0.721 ± 0.117	-1.472 ± 0.082	-1.338 ± 0.083	-1.399 ± 0.10
	aa	bc	bp	bt	cd	cs	fp	hp	mk	mp	pn	rt	sp	st	sd	se	tm	ta	tc
αaa	-1.912 ± 0.170	-6.179 ±12.455	-10.000 ± 0.914	-10.000 ± 0.536	-10.000 ± 0.292	-10.000 ± 0.111	X	-2.613 ± 0.703	-10.000 ± 0.018	-10.000 ± 0.199	X	-3.116 ± 0.690	-5.430 ± 6.224	-3.985 ± 2.744	X	-3.553 ± 2.334	X	-10.000 ± 0.157	-10.00 ± 0.15
αbc	-10.000 ± 0.763	-3.827 ± 3.060	-1.614 ± 0.711	-10.000 ± 0.119	-10.000 ± 0.106	X	-9.999 ± 5.998	-10.000 ± 0.983	-9.999 ± 1.872	X	-10.000 ± 0.182	-10.000 ± 0.087	-10.000 ± 0.166	-2.472 ± 0.732	X	-10.000 ± 0.155	-10.000 ± 0.095	-10.000 ± 0.274	-10.00 ± 0.04
αbp	-10.000 ± 0.201	-3.726 ± 3.764	-0.377 ± 0.194	X	-2.920 ± 1.075	-10.000 ± 0.593	-10.000 ± 1.011	X	-2.500 ± 0.384	-5.414 ±44.281	-10.000 ± 0.144	X	X	X	X	-1.059 ± 0.710	X	-10.000 ± 0.868	-10.00 ± 1.22
αbt	-2.677 ± 0.788	-5.767 ± 6.622	-9.998 ± 4.538	-1.578 ± 0.161	-10.000 ± 0.064	-3.370 ± 1.256	X	-5.438 ± 6.336	-10.000 ± 1.900	-10.000 ± 0.370	-4.462 ± 3.820	-10.000 ± 0.049	-10.000 ± 0.756	-9.992 ±12.714	-3.634 ± 1.678	-10.000 ± 0.053	-10.000 ± 0.044	X	-6.002 ± 5.99
αcd	-10.000 ± 0.023	-10.000 ± 0.375	-2.938 ± 0.487	-4.413 ± 0.960	-3.058 ± 0.149	-4.497 ± 1.166	X	-4.463 ± 1.112	-10.000 ± 0.025	-10.000 ± 0.089	-10.000 ± 0.232	-5.942 ± 1.912	-6.086 ± 5.653	-10.000 ± 0.016	-5.252 ± 2.754	-1.323 ± 0.654	-4.155 ± 0.805	-3.237 ± 0.325	-10.00 ± 0.04
αcs	-3.302 ± 1.264	-6.270 ± 12.771	-10.000 ± 0.934	-3.727 ± 1.363	-3.886 ± 1.503	-2.420 ± 0.237	-10.000 ± 0.090	-10.000 ± 0.048	-10.000 ± 0.012	-10.000 ± 0.687	-4.068 ± 2.369	-10.000 ± 0.254	-3.385 ± 1.963	-5.069 ± 2.374	-10.000 ± 0.586	-10.000 ± 0.039	-3.834 ± 0.915	-10.000 ± 0.154	-10.00 ± 0.01
αfp	-3.165 ± 1.465	-4.307 ± 1.947	-5.307 ±10.144	-10.000 ± 0.092	X	-10.000 ± 0.075	-0.785 ± 0.272	-10.000 ± 0.022	-10.000 ± 0.043	-10.000 ± 0.256	X	-3.657 ± 1.285	-10.000 ± 0.664	-10.000 ± 0.133	X	-10.000 ± 0.762	-10.000 ± 0.055	-4.402 ± 1.971	-10.00 ± 0.14
αhp	-10.000 ± 0.185	-10.000 ± 0.497	-3.515 ± 1.426	-10.000 ± 0.174	-10.000 ± 0.035	-10.000 ± 0.061	-2.696 ± 1.684	-2.375 ± 0.161	-10.000 ± 0.236	-9.995 ± 11.264	X	-10.000 ± 0.074	-2.697 ± 0.905	-9.996 ± 7.135	-10.000 ± 0.795	-10.000 ± 0.053	-10.000 ± 0.013	-10.000 ± 0.059	-3.798 ± 0.58
αmk	-10.000 ± 0.059	-10.000 ± 0.305	-4.192 ± 0.924	-3.664 ± 0.762	-10.000 ± 0.108	-6.175 ± 5.620	-10.000 ± 0.082	-10.000 ± 0.062	-2.231 ± 0.102	-2.144 ± 0.529	-10.000 ± 0.053	-4.413 ± 0.800	-4.335 ± 1.773	-5.405 ± 2.418	-4.051 ± 2.041	-10.000 ± 0.250	-10.000 ± 0.018	-10.000 ± 0.014	-10.00 ± 0.04
αmp	X	X	-9.999 ± 2.005	X	X	X	-10.000 ± 1.416	X	-10.000 ± 0.067	-0.941 ± 0.164	-3.334 ± 2.124	-3.567 ± 2.417	X	-10.000 ± 0.120	X	-10.000 ± 0.259	X	X	X
αpn	-10.000 ± 0.014	-5.426 ± 1.234	-10.000 ± 0.025	-10.000 ± 0.031	-10.000 ± 0.010	-10.000 ± 0.021	-10.000 ± 1.766	-10.000 ± 0.065	-10.000 ± 0.003	-10.000 ± 0.067	-2.866 ± 0.854	-6.080 ± 1.711	-10.000 ± 0.029	-4.559 ± 1.269	-4.553 ± 1.575	-5.000 ± 2.396	-4.092 ± 0.527	-10.000 ± 0.014	-10.00 ± 0.01
αrt	-10.000 ± 0.586	-9.998 ± 2.384	-2.647 ± 1.611	X	-4.573 ± 2.159	-5.322 ± 7.254	-9.999 ± 2.427	-10.000 ± 0.035	-10.000 ± 0.062	X	-10.000 ± 0.227	-2.535 ± 0.130	-10.000 ± 0.216	X	-10.000 ± 0.132	-10.000 ± 0.095	-10.000 ± 0.032	-10.000 ± 0.058	-10.00 ± 0.07
αsp	-10.000 ± 0.111	-8.109 ±110.460	-10.000 ± 0.239	X	-4.742 ± 4.860	-10.000 ± 0.164	X	-9.991 ±10.106	-10.000 ± 0.067	-3.236 ± 3.274	X	-10.000 ± 0.254	-2.103 ± 0.337	-10.000 ± 0.135	X	-10.000 ± 0.116	-9.999 ± 2.705	-10.000 ± 0.824	-10.00 ± 0.37
αst	-10.000 ± 0.725	X	-9.995 ± 4.138	-10.000 ± 0.033	-3.431 ± 1.261	-10.000 ± 0.076	-9.999 ± 3.387	-3.976 ± 1.982	-10.000 ± 0.093	-10.000 ± 0.165	X	-10.000 ± 0.946	-9.999 ± 3.684	-2.372 ± 0.188	X	-3.971 ± 5.078	X	-10.000 ± 0.105	-10.00 ± 0.04

Supporting Information. Zepeda, V., and C. Martorell. 2019. Fluctuation-independent niche differentiation and relative non-linearity drive coexistence in a species-rich grassland. *Ecology*.

Appendix S7. Temporal autocorrelation analysis of the lambdas for each study species

Blue dotted lines indicate the band within which correlations are not significant (α = 0.05). With the exception of *Microchloa kunthii*, none of the species show any significant autocorrelation between years. ACF: Autocorrelation function.



Aristida adscensionis

Bouteloua chondrosioides

Bouteloua polymorpha

Bulbostylis tenuifolia

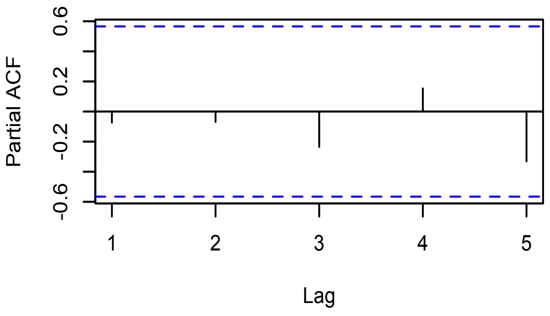
Crusea diversifolia

Cyperus seslerioides

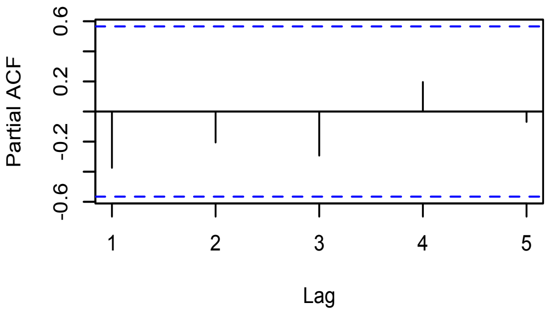
Florestina pedata

Heterosperma pinnatum

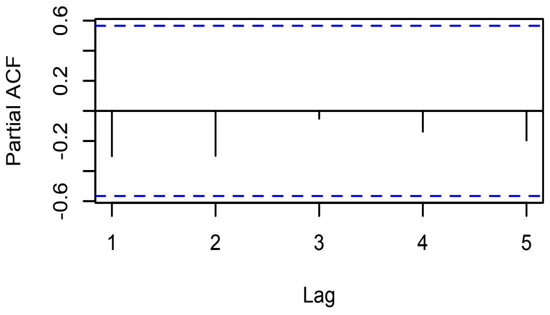
Sanvitalia procumbens



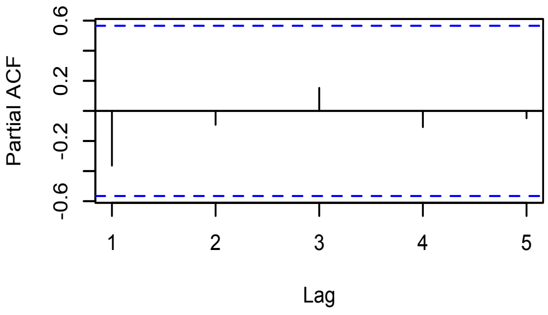
Sporobolus tenuissimus



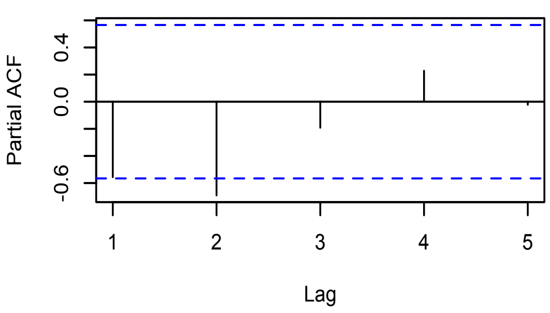
Stenandrium dulce



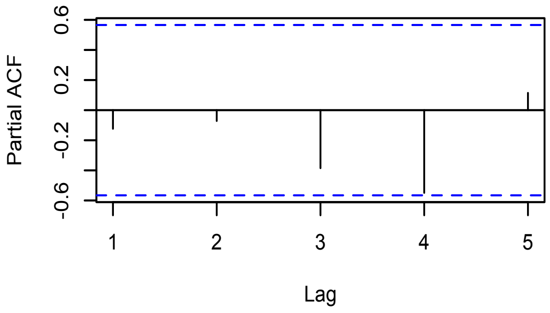
Stevia ephemera



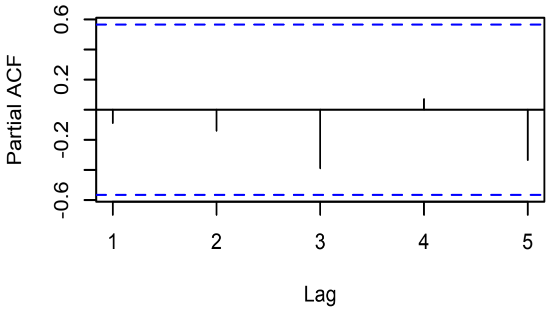
Microchloa kunthii



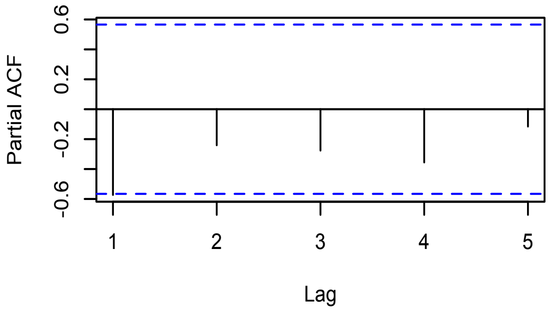
Muhlenbergia peruviana

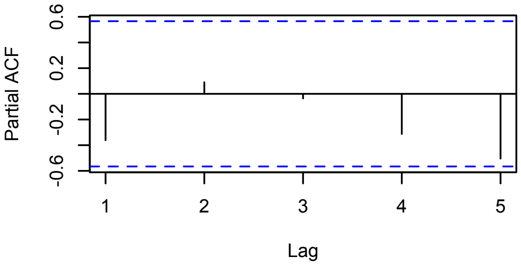


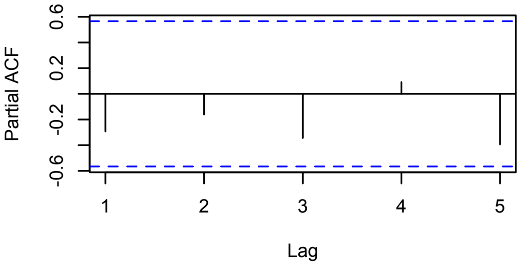
Plantago nivea

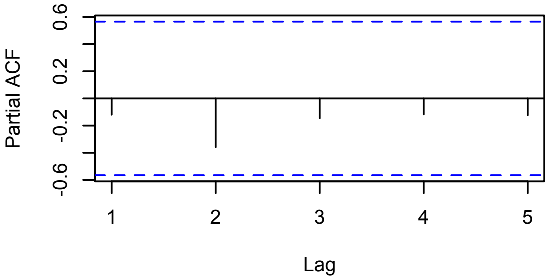


Ricardia tricocca




Tagetes micrantha


Tridax coronopifolia


Thymophylla aurantiaca

Capítulo I I

Effects of phylogenetic relatedness on fluctuation-dependent and fluctuation-independent coexistence mechanisms in multispecies communities

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E-ARTICLE

Effects of Phylogenetic Relatedness on Fluctuation-Dependent and Fluctuation-Independent Coexistence Mechanisms in Multispecies Communities

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Online enhancements: appendixes.

ABSTRACT: Evolutionary relatedness may hinder stable coexistence due to similar niches and nonlinear responses to competition. The mechanisms driving stability may respond differently to phylogenetic distance. Related species may be synchronic (have similar demographic responses over time), affecting fluctuation-dependent mechanisms: the storage effect should destabilize coexistence, and relative nonlinearity should be stronger due to increased fluctuations in competition. We tested these hypotheses using invasion analysis based on a model parameterized for 19 plant species from a semiarid grassland. Although weakly, coexistence stability increased with phylogenetic distance. Stabilization through fluctuation-independent niche differentiation was stronger between distant relatives as a result of weaker competition. Synchronicity was higher between close relatives, having the expected negative effects on the storage effect's contribution to coexistence. Relative nonlinearity was strong at both ends of the phylogenetic relatedness gradient but not in the middle. This may be the result of different nonlinear responses between distant relatives and of stronger fluctuations in competition due to synchronicity between closer relatives. The effect of phylogenetic distance on coexistence was almost negligible when pairwise species were analyzed, in accordance with previous research. Phylogenetic distance became more important as more species interacted, however, suggesting that evolutionary relatedness may be influential in species-rich communities.

Keywords: niche conservatism, competition, species coexistence, storage effect, relative nonlinearity, phylogenetic signal.

Introduction

How closely related species can stably coexist is a longstanding question in ecology. According to the competitive exclusion principle, species with the same niche cannot coexist for a long time (Gause 1934), whereas niche differences stabilize coexistence (Chesson 2000*b*; HilleRisLambers et al. 2012). Long-held views in ecology predict that close relatives will be less likely to coexist because their niches tend to be similar, as a result of phylogenetic signal (the tendency of closely related species to resemble each other), in the way that they use resources or in the predators that consume them (Webb et al. 2002).

In Chesson's coexistence framework, niche differences include all trait differences between species that cause them to limit themselves more than their competitors, resulting in intraspecific effects that exceed interspecific ones (Chesson 2000*b*, 2018). These differences stabilize coexistence because species have higher population growth rates when they are at low density, buffering them from extinction (HilleRisLambers et al. 2012). Particularly, greater intraspecific than interspecific competition has been recognized as a signature of niche differentiation (Levine and HilleRisLambers 2009). If there were phylogenetic signal in the niche, the competitive effect that a species has on itself would be quite similar to the competitive effect of their relatives. Thus, it would be expected that coexistence should be more stable between distant relatives.

According to modern coexistence theory, niche differentiation may be independent of temporal fluctuations, or else operate only when there is some form of variability over time (Chesson 2000*b*). Fluctuation-independent niche differentiation (FIND) encompasses any mechanism that operates within a place and time (Chesson 1994, 2000*a*). The most common examples are resource partitioning, predator partitioning, and frequency-dependent predation. These mechanisms promote coexistence because when a species is at very low density, it gains advantage by being less constrained by intraspecific effects (Chesson 2000*a*).

Fluctuation-dependent mechanisms are contingent on the temporal dimensions of the niche. If closely related species have similar niches, they are expected to respond

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in similar ways to temporal fluctuations. Thus, the demographic responses of relatives would be correlated over time, that is, relatives would be synchronized in their responses: when one species is able to grow, so is its relative, and unfavorable years would be detrimental for both. The mechanisms that promote fluctuation-dependent coexistence are relative nonlinearity (RNL) and the storage effect (SE; Chesson 2000*b*; Yuan and Chesson 2015).

Relative nonlinearity arises because species have different nonlinear responses to competition (Chesson 2018; Yuan and Chesson 2015). Jensen's inequality means that the long-term growth rates of each species will be affected differently by fluctuations: if response is concave up, the species is benefited by fluctuations and thus may persist in a system from which it would otherwise be excluded. The opposite occurs if the function is concave down (Chesson 2000*b*; Kuang and Chesson 2008). RNL is a measure of the differences in concavity between the species' responses to competition, and should be stronger if such responses differ more in their nonlinearity. RNL also increases with synchronicity, because the competitive contributions of different species will reinforce each other, leading to stronger fluctuations in competition over time (Yuan and Chesson 2015). Thus, stronger contributions of RNL to species coexistence are expected between close relatives because they tend to be more synchronic. RNL may also make important contributions to the coexistence of very distant relatives because the nonlinearity of their responses to competition may have become very different over the course of evolution. Note that when RNL favors some species, it necessarily has a negative effect on the others (Chesson 1994).

The storage effect arises through an interaction between the environment and competition: because the effects of competition are buffered in bad years, the gains obtained in favorable periods compensate for bad-year losses that would otherwise lead to extinction (Chesson 1994). There are three conditions necessary for the SE to occur: (1) species-specific responses to the environment, meaning that low synchronicity is required (Chesson 2000*b*, 2008), (2) environment-competition (E-C) covariance, which measures to what extent the ability of a species to benefit from favorable environmental conditions is inhibited by competition (Chesson 2000*b*; Chesson et al. 2004; a positive E-C covariance constrains population growth rate fluctuations, and if covariances become weaker or negative when a species' density drops, it may take advantage of environmentally favorable periods with low competition, leading to its recovery; Chesson 2003; Chesson et al. 2004), and (3) competition buffering, which is when the joint negative effect of adverse years and competition on the population growth rate is smaller than the sum of both effects separately (Chesson 1994). This means that benefits gained during favorable years are not canceled out by population decline during unfavorable periods (Chesson and Huntly 1988). Strong positive contributions of SE to coexistence are not expected between close relatives, because favorable years for a species may also be favorable for their relatives. If so, species would experience strong competition during favorable periods, precluding recovery when they are at low density.

Although many studies have tested whether there is a phylogenetic pattern in competition among species (Cahill et al. 2008; Vamosi et al. 2009; Anderson et al. 2011), most studies have focused on the way that species use resources without quantifying the consequences on long-term population growth rates (Adler et al. 2010). To date, only a few studies have measured changes in competition with phylogenetic distance and their consequences for stable coexistence (Narwani et al. 2013; Godoy et al. 2014; Germain et al. 2016; Gallego et al. 2019). However, the specific mechanism from which stabilization arises remains unknown. The contributions of fluctuation-dependent mechanisms to coexistence over phylogenetic gradients have so far been overlooked, both from the theoretical perspective and in empirical studies. Moreover, previous work has focused on evaluating the effect of phylogenetic distance on the coexistence of species pairs, ignoring the phylogenetic patterns that could arise in multispecies communities. This is important because (1) stability usually diminishes with species richness in model systems (May 1972) and (2) the strength of some mechanisms is related to the number of interacting species. For instance, as more species are interacting, RNL is expected to become stronger (Yuan and Chesson 2015). Fluctuation-independent niche differentiation is expected to become small as species richness increases due to the impossibility of niches to become different from each other in an already-saturated niche space (Gravel et al. 2006).

In this study, we assessed the effect of phylogenetic relatedness on the strength of FIND, SE, and RNL. Based on the literature, we propose a novel framework for the relationship between evolutionary relatedness and fluctuation-dependent coexistence mechanisms: (1) Due to phylogenetic signal in the niche, pairwise competition and synchronicity should diminish with phylogenetic distance. (2) Stable coexistence through the SE is not expected between close relatives due to more positive E-C covariance and increased synchronicity. (3) Relative nonlinearity could be strong between close relatives due to high synchronicity, but also between distant species due to increasing differences in the nonlinearity of responses to competition. Finally, we expect (4) stability to be weaker between closely related species because close relatives are ecologically more similar, both in terms of their fluctuation-dependent and fluctuation-independent responses to the environment. To test these hypotheses, we analyzed how pairwise competition, synchronicity, and the ingredients of the SE depend on phylogenetic relatedness. We also assessed the effects of phylogenetic distance between species pairs on each one of the coexistence mechanisms by means of invasion analysis. The same was done for systems where there were multiple species interacting. Finally, we analyzed how synchronicity affects coexistence by simulating communities in which all the species have identical or very different responses to environment fluctuations.

Methods

Our study was conducted in Concepción Buenavista, Oaxaca, Mexico. The climate is semiarid, with a mean annual temperature of 16°C and an annual rainfall of 530.3 mm (Martorell et al. 2017). The elevation is 2,275 m asl. The vegetation is a short (<10 cm tall) grassland dominated by *Bouteloua* spp. (Cruz-Cisneros and Rzedowski 1980).

Measurement of Coexistence Mechanisms

We used a model that describes the population dynamics of the 19 most common species of the grassland (11 annuals and eight perennials) published by Zepeda and Martorell (2019). The model for each focal species j is a modified version of the Hassell model where the intrinsic growth rates, $\lambda_{j,t}$, are allowed to vary every year t, the intra and interspecific competitive interactions are included, and the exponent was modified to permit annual changes in the intensity of competition:

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1 + \sum_{k} \alpha_{j,k} N_{t,k}\right)^{\exp(a_j + b_j \ln \lambda_{j,t})}}, \qquad (1)$$

where $N_{j,t}$ is the abundance of species j at time t, $\alpha_{j,k}$ is a per capita coefficient determining the competitive effect of species k on species j, and b_j determines the change in the exponent a_j as a result of environmental fluctuations. A positive value of b_j would buffer competition in unfavorable years, as required by the SE. The per capita intensity $\alpha_{j,k}$ of intra- and interspecific competitive interactions, as well as a_j and b_j, were assumed to be constant over time. All the parameters were estimated maximizing the likelihood of a nonlinear regression of the observed $N_{j,t+1}$ on $N_{j,t}$, using equation (1). The data came from annual measurements of the number of individuals of every plant species in 4,000 quadrats measuring 0.1 m × 0.1 m over 13 years. The sampling unit reflects the scale over which interactions occur given the small sizes of the plants (Martorell and Freckleton 2014). More details about the experimental design and model fitting are explained in Zepeda and Martorell (2019).

Stable coexistence arises when each species, when rare, is able to invade a steady-state community containing all other species (Chesson 2000*b*). Thus, we used invasion analysis to quantify the stability of coexistence. In these analyses, one species—the invader, indicated by subscript i—is removed from the community (Chesson 1994; Schreiber et al. 2011). All other species, known as residents, are allowed to come to equilibrium in the invader's absence (Chesson 1994). The long-term growth rate of the invader at low density is calculated ($\bar{r}_i$) under such equilibrial conditions. The procedure is repeated for every species in the community. Following the invasibility principle, all species in the community can coexist if they can invade the system, that is, if all $\bar{r}_i$ are positive (Chesson 1994). To estimate the structure of the community at equilibrium, we simulated the population dynamics of the residents by iterating equation (1). To include environmental fluctuations, in each iteration we selected randomly and with equal probabilities one out of the 12 annual transitions that we observed. The $\lambda_{j,t}$ values for that transition were used in the projection of population sizes into the next year. The model was iterated 10,000 times to allow the residents to reach their stationary densities and then iterated 200,000 more times, for which we calculated the growth rate of the invader as the right-hand side of equation (1). The logarithms of these numbers were averaged to obtain $\bar{r}_i$.

We conducted three sets of simulations to divide $\bar{r}_i$ into different coexistence mechanisms (Zepeda and Martorell 2019). In the first one, we used the field-estimated parameters and obtained $\bar{r}_{i,\mathrm{obs}}$. In the second one, we set $b_i = 0$ for the invader to eliminate the SE and calculated $\bar{r}_{i,b=0}$. The value of a_i in this set of models was modified so that the mean of the population growth model's exponent over time remains constant and equal to that of the model with nonzero b. This has been shown to be an appropriate procedure to estimate RNL accurately (Zepeda and Martorell 2019). In the third set, the λ values of all the species were set to their respective geometric means, making the environment constant, and obtained $\bar{r}_{i,\mathrm{const}}$. This procedure removes any exogenous fluctuation in the system, thus eliminating both the SE and (in the absence of endogenous fluctuations, which do not seem to occur in our system; Zepeda and Martorell 2019) the RNL. We then estimated the SE as $\mathrm{SE} = \bar{r}_{i,\mathrm{obs}} - \bar{r}_{i,b=0}$, the RNL as $\mathrm{RNL} = \bar{r}_{i,\mathrm{const}} - \bar{r}_{i,b=0}$, and the fluctuation-independent niche differentiation as $\mathrm{FIND} = \bar{r}_{i,\mathrm{obs}} - \mathrm{SE} - \mathrm{RNL}$. In this procedure, FIND is a measure of how much greater the niche differentiation is than the minimum required for stable coexistence given the fitness differences between species. Thus, we cannot estimate the effects of equalizing mechanism on coexistence using this procedure (Chesson 1994; Zepeda and Martorell 2019).

Phylogenetic Effects on the Conditions of SE and Competition Strength

For all of our analyses, we used the phylogenetic tree of the species in our study obtained by Martínez-Blancas et al.

(2018) through Bayesian analysis based on two plastid DNA fragments: *rbcL* and *matK*. We analyzed how each ingredient of the SE was affected by species relatedness. To do so, we tested whether there was a phylogenetic signal in b_j (i.e., competition buffering) by means of a Pagel's λ using phytools (Revell 2012) for R. Synchronicity between two species was measured as the Euclidean distances between their z-transformed $\lambda_{j,t}$ values over time. Greater distances imply lower synchronicity. To assess whether close relatives are more synchronic, we used a Mantel test using synchronicity and phylogenetic distances.

The effect of competition on species performance is likely to be stronger when more species are interacting. Thus, for each focal species, we computed the E-C covariances (for details, see Zepeda and Martorell 2019) with each other species and with different numbers of associated species. We ran 1,500 simulations for each species as an invader with a different random sample of three, six, and nine associated species. In each run, we quantified the mean phylogenetic distance.

Using a generalized linear mixed model (GLMM), we regressed the E-C covariance on the mean phylogenetic distances and the number of associated species as fixed effects variables. We included the identity of the invader as a random effect because species may differ in the strength of the E-C covariance that they experience and respond differently to mean phylogenetic distance and community richness. We fitted the most complex model, which was the one that included the effect of the mean phylogenetic distance, the number of associated species, and their interaction, as well as models containing all the subsets of these variables. We tried five different structures for the random effects: where the fitted models for each species differ (1) only in the intercept, (2) in the intercept and the slope of the effect of mean phylogenetic distance, (3) in the intercept and the slope of the effect of the number of associated species, (4) in the intercept and both slopes, and (5) in the intercept, both slopes, and their interaction. Preliminary analyses showed that random effects should be included in all analyses. We computed the Akaike information criterion (AIC) for each of the models and selected the one with the smallest AIC value as the model with the best support from the data (Burnham and Anderson 2002). All regressions were performed using lme4 (Bates et al. 2015). Once we chose the best model, we calculated a 95% confidence interval by bootstrapping for the regression model. All analyses were computed in R (R Core Team 2018).

Finally, we tested whether interspecific competition was stronger between closer relatives. To do this, we performed a GLMM, setting strength of competition ($\alpha_{j,k}$ values) as the response variable and phylogenetic distance as the fixed effect variable. The identity of focal species was included in all the regressions as a random effect, following the same procedure used for the analysis of synchronicity.

Effects of Phylogenetic Distance on Coexistence

The strength of stable coexistence, as well as the different mechanisms that contribute to it, relies on the sensitivities and the competitive ability of the interacting species. We thus estimated $\bar{r}_i$ and its components for every pair of species. The number of species in the community is also thought to affect coexistence mechanisms (Spaak et al. 2019).We thus used the same simulations employed to estimate E-C covariance, in which communities with different number of species and mean phylogenetic distance were analyzed. Using GLMM, we regressed the strength of each mechanism (SE, RNL, or FIND) and the invasion growth rates ($\bar{r}_i$) on the mean phylogenetic distances and number of associated species as fixed effects variables and tried the same species-specific (random effect) structures considered for the analysis of E-C covariance. We included the identity of the invader as a random effect because species may depend on different coexistence mechanisms and respond differently to mean phylogenetic distance and community richness. We used the method by Johnson (2014) to obtain a measure of the variance explained by the models. With this procedure, we can estimate two R^2 values, the marginal R^2_{m}, which includes only fixed effects, and the conditional R^2_{c}, which also includes random effects.

Additionally, we assessed whether our results are robust in face of the relatively large uncertainty in parameter values (Zepeda and Martorell 2019). To do so, we produced new parameter values randomly from a multivariate normal distribution. We repeated the simulations of community dynamics using the randomly parameterized models, and we obtained the respective estimates of $\bar{r}_i$, SE, RNL, and FIND. Using these data, we fitted the GLMM, relating coexistence mechanisms to mean phylogenetic distance and species richness as before (see app. S1; apps. S1–S3 are available online).

Effects of Synchronicity on Coexistence

The correlation between the $\lambda_{j,t}$ values of different species over time is a proxy of how similar their responses are to the environment. The more positive the correlation is, the more similar the species are in their performance over time. They are therefore more synchronic.

To simulate a community with synchronic species, we sorted the λ values from largest to the smallest. In this way, all species experienced in the same year the largest population growth, then the second largest, and so on, maximizing the synchronicity between them. Using the new values, we quantified the contribution of different coexistence mechanisms, following the procedure described above.

We also simulated communities with low synchronicity by randomizing the $\lambda_{j,t}$ values of each species independently over time. We performed this procedure 30 times. On each run, we quantified the strength of the coexistence mechanisms and then calculated the mean of each coexistence mechanism and $\bar{r}_i$ for each focal species over the 30 simulations.

Results

In all cases, the structure of the random effects of the best models contained phylogenetic distance and (whenever possible) number of associated species and their interaction, indicating that the effect of phylogenetic distance differed between species and depended on community richness. The smallest ΔAIC for a model with simpler random effects specification was 267.9 (table S2.1; tables S1.1, S2.1–S2.5 are available online).

Closely related species tended to compete more intensely and were more synchronic than distantly related ones. We found a negative relationship between phylogenetic distance and per capita competition (α_{jk}). Models without phylogenetic distance were not supported by the evidence ($\Delta\mathrm{AIC} > 3.2$; table S2.4). However, this model explained a relatively small fraction of the variance ($R^2_\mathrm{m} = 0.07$). The Euclidean distances between the lambda values of each species were also larger as more distant relatives were considered (Mantel's $r = 0.316$, $P = .001$).

Evolutionary relatedness also affected the ingredients of the SE. There was phylogenetic signal in competition buffering (b; Pagel's $\lambda = 0.59$, $P = .001$). With only one exception, monocots had $b < 0$, and just one dicot experienced competition buffering (fig. S2.1; figs. S1.1, S1.2, S2.1, S2.2, S3.1–S3.19 are available online). The low-density E-C covariances were positive on average, and diminished with mean phylogenetic distance (table 1; fig. 1; the best model without mean phylogenetic distance had a ΔAIC of 3.4). Moreover, the effect of mean phylogenetic distance was stronger as the number of associated species increased (fig. 2). Again, the R^2_m was low (0.04). However, when parameter uncertainty was considered, the evidence suggested that the covariances were independent of phylogenetic distance (app. S1).

Models where $\bar{r}_i$ and FIND increased with phylogenetic distance but decreased with number of associated species were the ones with the strongest support by the data (table 1; fig. 2). The best models without mean phylogenetic distance had a ΔAIC of 1.8 for FIND, suggesting reasonable, although disputable, support for the inclusion of mean phylogenetic distance in the model. The R^2_m was also quite low (0.03), indicating that despite the general trend, it is possible to observe communities composed of closely related species that are strongly stabilized by FIND, and vice versa (for the detailed scatterplots, see app. S3). There was also a very large R^2_c (>0.76), indicating very large differences between species. In fact, FIND diminished with mean phylogenetic distance in six of the 19 species. When accounting for parameter uncertainty, the same patterns were observed. It remained clear that $\bar{r}_i$ and FIND change with species richness, and the models that included phylogenetic distance still had some support (app. S1), although the evidence became weaker.

The mean of RNL was close to zero and decreased with mean phylogenetic distance, but the best model did not include numbers of associated species (table 1; fig. 2). The best models without mean phylogenetic distance had a ΔAIC of 1.9 and R^2_m was very small (0.001), again casting doubts on whether mean phylogenetic distance should be considered. However, when the individual responses of species were considered, RNL was stronger at both ends of the phylogenetic distance gradient than in its center, and this pattern became stronger as more species were interacting (fig. 3). The mean of the SE depended only on the number of species in the community (table 1). The best model with mean phylogenetic distance had a ΔAIC of 0.4, indicating a large

Table 1: ΔAIC values for the models that describe effects of mean phylogenetic distance (D) and number of associated species (A) on the strength of long-term, low-density population growth rate ($\bar{r}_i$), fluctuation-independent niche differences (FIND), relative nonlinearity (RNL), storage effect (SE), and low-density environment-competition covariance (E-C cov)

Model	$\bar{r}_i$	FIND	RNL	SE	E-C cov	No. estimated parameters
Intercept only	13.1	12.9	1.2	4.1	10.9	1
A	1.5	1.8	1.9	0	3.4	2
D	14.0	14.0	0	1.9	11.8	2
A + D	3.3	3.7	.2	1.6	3.1	3
A × D	9.5	10.6	2.1	.4	6.5	2
A + A × D	0	.1	3.9	.5	4.8	3
D + A × D	11.4	12.5	.5	2.1	7.9	3
A + D + A × D	.2	0	2.2	1.6	0	4

Note: In all cases, the random effects structure of the best model contained different A + D + A × D terms for each focal species. Models with ΔAIC = 0 were the models with the best support on the data. The smallest ΔAIC for models with a different random effects structure was 268, so they can be discarded. To find all alternative formulations for the random effects, see table S2.1. All models were fitted using 85,784 data points. AIC = Akaike information criterion.

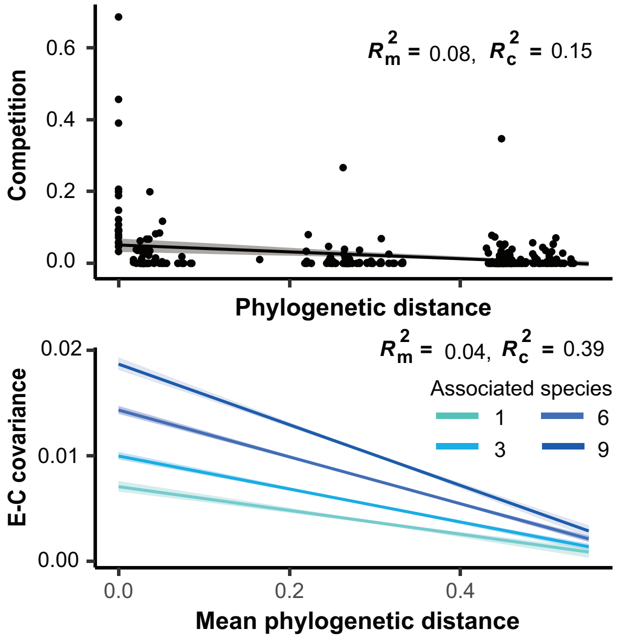

Figure 1: Effect of phylogenetic distance on pairwise competition strength, synchronicity, and low-density environment-competition (E-C) covariance with different numbers of associated species. Ribbons correspond to 95% confidence intervals.

uncertainty about the inclusion of this parameter in the model. Its effect would be negligible either way, as the R^2_m was tiny (0.0005). Three species showed negative contributions of the SE, which diminished with phylogenetic distance. More negative SE values were observed in the most speciose assemblages (fig. 3). As before, the relationship between fluctuation-dependent coexistence mechanisms remained unaltered by including parameter uncertainty (app. S1).

The contribution of FIND to coexistence did not change with synchronicity. The strongest contributions of RNL to coexistence, either positive or negative, tended to be stronger as synchronicity increased. In the species where the SE had an effect, it was slightly more negative when species were forced to be synchronic (fig. 4).

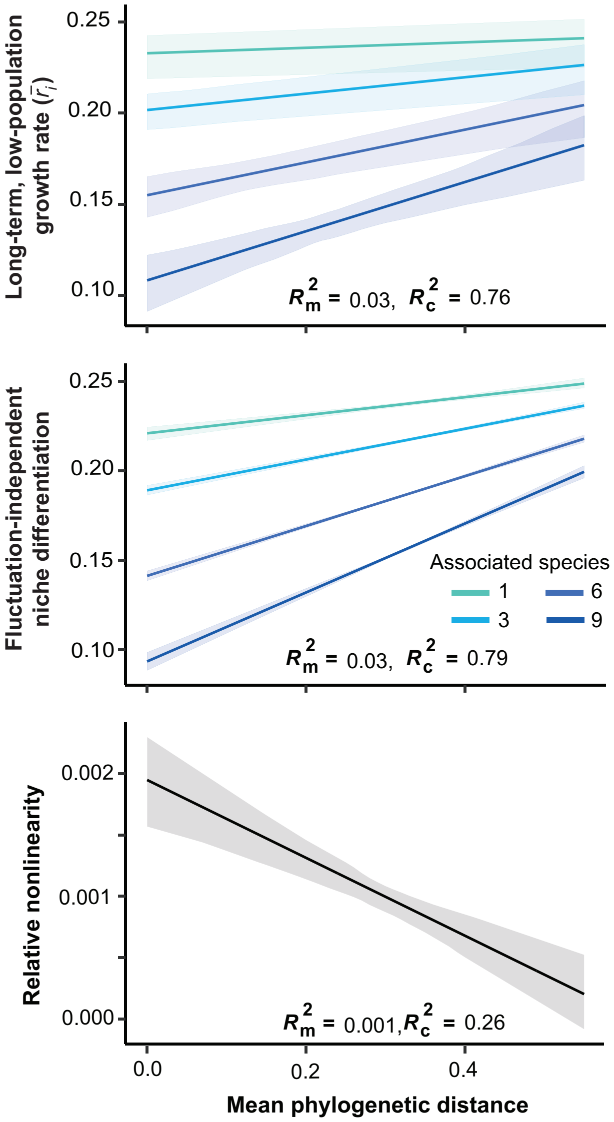

Figure 2: Relationship between phylogenetic distance and the long-term, low-density population growth rate $\bar{r}_i$ (*top*), fluctuation-independent niche differentiation (*middle*), and relative nonlinearity (RNL; *bottom*) for different numbers of associated species. Phylogenetic distance did not affect the mean storage effect. The effects of RNL were independent of how many species interacted. Ribbons correspond to 95% confidence intervals.

Discussion

In this study we assessed whether phylogenetic relatedness determines the strength of the mechanisms that underlie stable coexistence. Consistent with our expectation, we found that as species diverge from one another along the phylogenetic distance gradient, the mechanisms that promote stable coexistence become stronger. However, the effect of mean phylogenetic distance on coexistence was weak, perhaps explaining why this pattern has remained elusive in previous studies. In this work, the pattern is not as clear either, because even if the best model included the mean phylogenetic distance, some alternatives did not. The effect of phylogenetic relatedness was almost negligible when we analyzed species pairs, becoming more important as more species interacted. This suggests that evolutionary relatedness is irrelevant when considering species pairs but may be influential in multispecies communities.

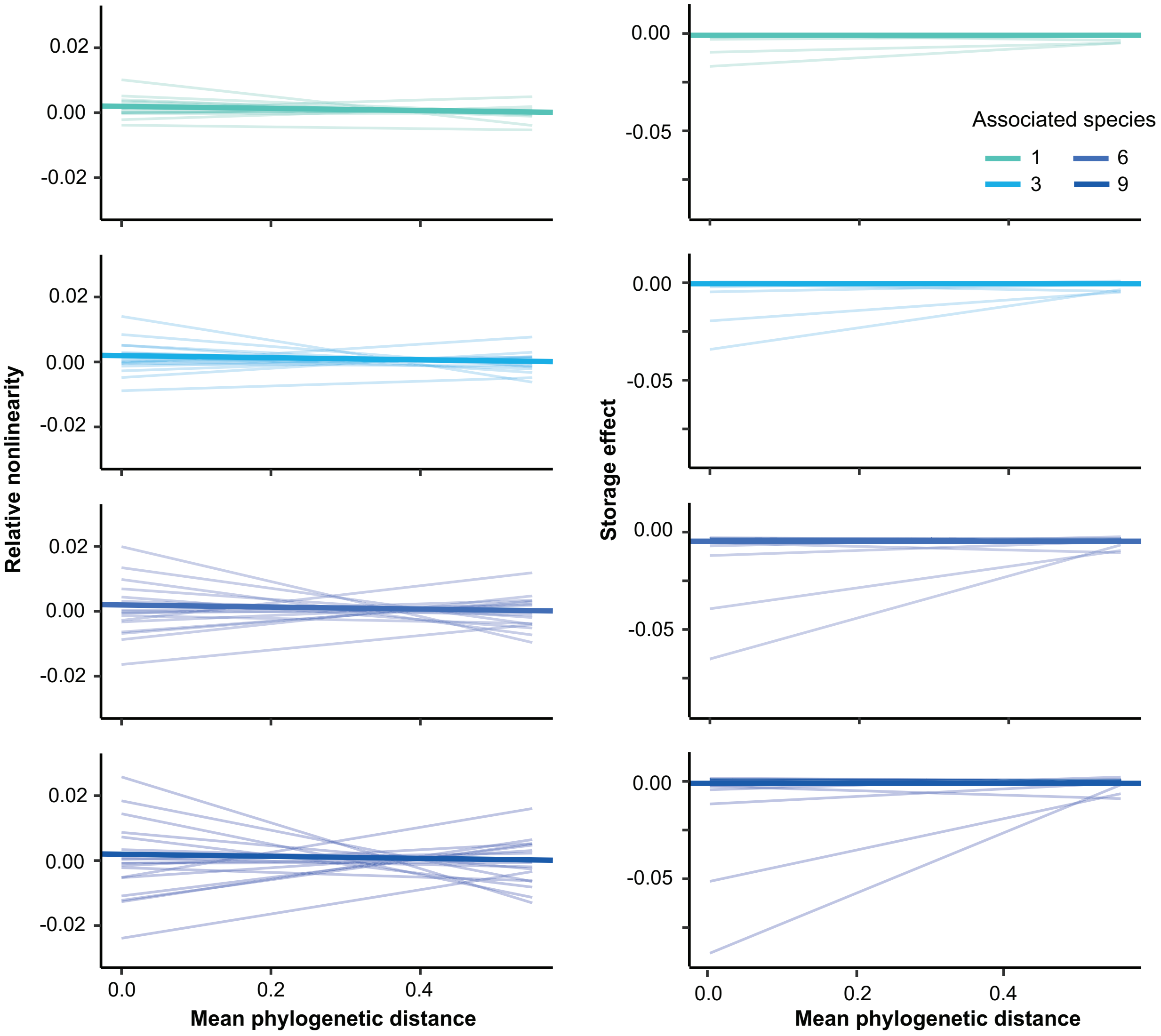

Figure 3: Relationship between the mean phylogenetic distance and the fluctuation-dependent mechanisms (relative nonlinearity [RNL] and storage effect) for each study species depending on the number of associated species. The thick line shows the mean response. Variance explained by the storage effect model was $R^2_{\mathrm{m}} = 0.0005$ and $R^2_{\mathrm{c}} = 0.63$; explained variance for RNL was $R^2_{\mathrm{m}} = 0.0015$ and $R^2_{\mathrm{c}} = 0.26$.

From our model, we concluded that FIND is the driving force for the coexistence of the species considered here (Zepeda and Martorell 2019). This results from a greater intraspecific competition relative to interspecific competition. Relative nonlinearity is the second mechanism that contributes the most to stable coexistence, and the SE has a negligible or destabilizing effect on diversity maintenance (Zepeda and Martorell 2019). The same patterns can be seen in the present analyses.

Stability of coexistence (measured as the long-term, low-density growth rates, $\bar{r}_i$) diminished with the number of species in the community, probably as a result of stronger interspecific competition as more species interact. Stable coexistence through FIND and SE was hindered when more species were interacting. Intraspecific competition was always stronger than interspecific competition, resulting in a large FIND. However, as the number of species in the community increase, their competitive effects add up (eq. [1],) and total interspecific competition increases, as has been observed empirically in some systems (Valone and Hoffman 2003; HilleRisLambers et al. 2004). Thus, the gap between the strengths of intra and interspecific competition diminishes with species richness, reducing stability. This is at odds with the idea that, in complex networks of competitors, indirect

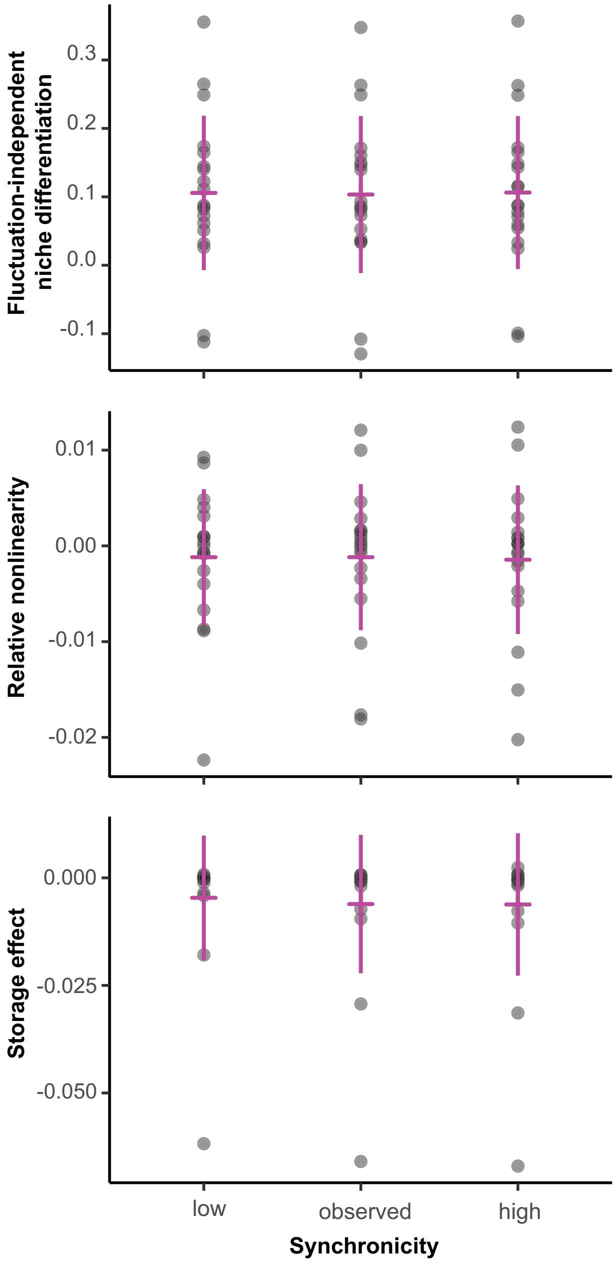

Figure 4: Magnitude of fluctuation-independent niche differentiation (*top*), relative nonlinearity (*middle*), and storage effect (*bottom*) for the observed data and after forcing species to have low or high synchronicity. Horizontal lines show the mean of the values, and vertical lines show the standard deviation.

positive interactions that stabilize coexistence arise (HilleRisLambers et al. 2004; Levine et al. 2017).

Effects of Phylogenetic Distance on Coexistence

All the factors that affect coexistence mechanisms depended on evolutionary relatedness: competition and synchronicity were stronger between closer relatives, the E-C covariance changed with phylogenetic distance (fig. 3), and the strength of competition buffering showed phylogenetic signal. Nevertheless, there was a large amount of unexplained variation related to interspecific variability and the considered species pairs. As a result, the strength and relative importance of the different coexistence mechanisms changed depending on the mean phylogenetic relatedness of the communities, although the unexplained variation increased substantially. Values for R^2_m were ≤ 0.03. We must consider that the R^2_c values were quite large, indicating that differences between species could explain most of the variation. Under such conditions, fixed effects can explain only a small proportion of the variance. In any case, FIND explains 12% of the variation that remains after removing the effect of the species, which is still a relatively small proportion. This, altogether with the relative support for models that lack phylogenetic distance in our analyses (especially when considering parameter uncertainty; see app. S1), suggests that the effect of phylogenetic distance on coexistence is extremely dependent on the study species and that the general trend is weak. However, it must be noted that in the bootstrapped models, regardless of whether they include parameter uncertainty, the confidence intervals show a clear effect of mean phylogenetic distance on coexistence mechanism strength (figs. 2, S1.1).

Coexistence between species tended to be more stable as phylogenetic distance increased, mostly as a result of lower competition between distantly related species. The intensity of per capita competition (α_{jk}) was higher between more closely related species, suggesting that their niche differences were small. The idea that closely related species compete more strongly than distantly related ones has been a central topic in community ecology, as close relatives are expected to share similar resources, habits, and traits (Prinzing et al. 2001; Wiens and Graham 2005). Although empirical evidence about the "competition relatedness hypothesis" is mixed (Cahill et al. 2008), our results support it. Because competition between distantly related species was weaker, FIND tended to increase with mean phylogenetic distance. Stable coexistence between close relatives is thought to be less likely because, when a species becomes rare, it is easily replaced by its closest relatives, making it difficult to recover (Stump 2017). Nevertheless, the large variability around the relationship between the mean phylogenetic distance and FIND means that sometimes even close relatives can coexist more stably than distant ones.

There was also a trend for phylogenetic relatedness to affect coexistence through fluctuation-dependent mechanisms. Positive and negative contributions of RNL experienced by different species should cancel out, resulting in an average that is close to zero regardless of phylogenetic relatedness, as seen in figure 1. However, it is not the average but the behavior of the different species about the average that is of interest when analyzing RNL. The different responses of each species are considered in the random effects, which are certainly affected by mean phylogenetic distance and its interaction with species richness (ΔAIC of the models without mean phylogenetic distance in the random effects $=$ 3,411). If we consider species separately and not just their means, RNL should contribute strongly to coexistence of distant relatives because they may show different nonlinear responses to competition. Large values were also expected to occur between close relatives because their demographic behaviors are more synchronic, resulting in high variability in competition strength (Yuan and Chesson 2015). Our results would seem to be consistent with these ideas, because the largest RNL values were observed at both ends of the phylogenetic gradient (fig. 3). However, our results suggest that RNL increases only marginally with synchronicity (fig. 4), casting doubt on whether the larger RNL values observed between close relatives were due to the similarity in their responses to environmental fluctuations. Relative nonlinearity also became stronger as the number of species interacting increased, supporting the idea that it may be an important driver in species-rich communities (Yuan and Chesson 2015).

Evolutionary relatedness is expected to have an effect on the SE if its ingredients show phylogenetic signal. In the present study, monocots buffered competition while the dicots did not (fig. S2.1). This means that when we focus on a monocot and the mean phylogenetic distance of the community is small, all species (other monocots) experience buffering. In principle, widespread buffering may affect the SE. In the lottery model, this effect is positive (see Chesson 1994, eq. [90]), so species belonging to a clade where buffering is widespread could experience stabilizing SEs. However, we did not observe positive SEs between close relatives.

It appears that E-C covariances explain most of the patterns that we observed in the SE. Negative values are associated with positive E-C covariances when species are at low density (Yuan and Chesson 2015). The three species with strong negative SEs (*Muhlenbergia*, *Cyperus*, and *Bulbostylis*) were the only ones with competition buffering and positive E-C covariances at low density (fig. S2.2). Synchronicity is expected to increase the E-C covariances (Yuan and Chesson 2015), which may explain why the SE was slightly more negative when all species were forced to respond similarly to environmental fluctuations (fig. 4). Other studies have also reported the SE to decrease when the environmental responses of different species are similar (Chesson 2003). A more negative SE as the number of species increased is in line with our finding that E-C covariances became more positive as the number of associated species increased. In any case, we did not find that SE changes with mean phylogenetic distance, and it therefore does not seem to contribute to the coexistence of close or distant relatives.

Concluding Remarks

Our results support the theoretical expectation that distant relatives are more likely to coexist stably than close ones. Contrastingly, no evidence for such a pattern has been found in most of the previous studies (Usinowicz et al. 2012; Narwani et al. 2013; Godoy et al. 2014; Gallego et al. 2019), with the exception of Germain et al. (2016). In part, this disagreement between our results and those previously published may be explained by considering the number of species studied: when we analyzed pairs of species, as all of the previous studies did, we also found very weak effects of mean phylogenetic distance on coexistence. Thus, conclusions drawn from studies on the basis of species pairs are unlikely to remain valid in highly diverse communities. Moreover, mean phylogenetic distance explained very little of the variance in stabilization, indicating that its effects are difficult to detect and that they depend very strongly on the study species.

Although it has been shown that species are less likely to coexist stably in multispecies communities (May 1972), less attention has been focused on how species richness affects the strength of the mechanisms that determine stability. The reduction in the intensity of FIND, and the more negative contributions of the SE as more species are interacting, contributed to destabilizing coexistence in rich communities, maybe because niche space is limited (Gravel et al. 2006). As there are more species in the community, there is less of a chance to find resources or opportunity windows for which competition is low. In contrast, rich communities had larger positive and negative contributions of RNL as species richness increased. We must bear in mind that RNL is negatively correlated with FIND in our study system (Zepeda and Martorell 2019), increasing the growth rates of species that are less favored by niche differentiation. This opens the possibility that RNL facilitates multispecies coexistence, and may allow closely related species to persist even when their niches are similar. However, phylogenetic distance played a minor role in determining coexistence. This may be due to the lack of phylogenetic signal in functional attributes, which may be more important than evolutionary relatedness in determining coexistence (Angert et al. 2009; Kraft et al. 2015). At the study site, granivory by ants determines plant population dynamics to a large degree (García-Meza et al. 2021). These granivores are generalists and thus may blur the effects of species relatedness. Simple error in the parameter estimates may also contribute to the large amount of noise in our data. Other processes not considered in our study, such as positive interactions (Valiente-Banuet and Verdú 2007) and demographic stochasticity (Hubbell 2001), may furthermore affect coexistence of close relatives in species-rich communities (Mayfield and Levine 2010).

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Statement of Authorship

C.M. and V.Z. conceived research and developed the code. V.Z. analyzed the data and wrote the manuscript. Both authors read and approved the manuscript.

Data and Code Availability

All code and data have been deposited in Zenodo (https://doi.org/10.5281/zenodo.4465178).

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A storm looms over the grassland at Concepción Buenavista, Oaxaca, Mexico. Photo: C. Martorell.

Online Supplement: Effects of phylogenetic relatedness on fluctuation-dependent and independent coexistence mechanisms in multispecies communities

The American Naturalist

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Online Appendix S1: Effect of parameter uncertainty

When considering the effects that parameter uncertainty may have on our analysis of the relationship between coexistence and phylogenetic distance, we must face a complicated error structure in the high-dimensional, non-linear model that describes de dynamics of each population. This makes it impossible to proceed analytically, so a numerical method is required. The approach that we used to incorporate uncertainty was to generate random parameters extracted from the multivariate distribution of the parameters in each model, and run the coexistence analyses using the random parameters. This procedure was repeated thousands of times.

Assuming that the parameters are normally distributed, the mean equals the mode, i.e., the maximum likelihood solution, and the variances are the parameter standard errors squared. The variance-covariance matrix was provided by ADMB (Fournier et al. 2012), the program used to fit the models (Zepeda and Martorell 2019). However, in many instances we did not know the mean and standard error of the parameter, but those of its logarithm. This is because these parameters are only meaningful if they were positive, as it happens for instance with population growth rates (otherwise the model will produce negative population sizes). In such cases, it is useless to consider negative values during model fitting. One common way to bound a parameter β to positive values is to estimate the maximum likelihood value of $\beta' = \ln(\beta)$ instead of estimating β directly, and to use $e^{\beta'}$ instead of β throughout the fitting process. Because the exponential function yields only positive values, β is bounded between 0 and infinity, as required.

It is important to note that the standard errors of the parameters in complex models are usually impossible to calculate. Instead, they are approximated indirectly from the second derivatives H' of the likelihood function evaluated at the maximum likelihood estimate. Statistical software usually calculates the standard errors under the assumption that the parameterβ' is normally distributed with mean $\widehat{\beta'}$ = maximum likelihood estimate of parameter, and standard error σ'. Thus,

$$H' = \frac{\partial^2}{\partial \beta'^2} \frac{e^{-\frac{\left(\beta' - \widehat{\beta'}\right)^2}{2\sigma'^2}}}{\sigma'\sqrt{2\pi}} \Bigg|_{\beta' = \widehat{\beta'}} = -\frac{1}{\sqrt{2\pi}\sigma'^3} \quad . \tag{1}$$

which means we can back-engineer the standard errors provided by ADMB to obtain the second derivatives H' of the likelihood function at $\widehat{\beta'}$. These second derivatives are numerically estimated, and are independent of the actual distribution of β'. This is important because we are assuming that β, and not β', is normally distributed. Let $\hat{\beta}$ and σ be the mean and standard error of β. Thus, the likelihood function for β' would be

$$\mathcal{L}(\beta') = \frac{e^{-\frac{\left(e^{\beta'} - \hat{\beta}\right)^2}{2\sigma^2}}}{\sigma\sqrt{2\pi}} \tag{2}$$

Which means that the actual function relating H' to σ would be

$$H' = \frac{\partial^2}{\partial \beta'^2}\mathcal{L}(\beta')|_{\beta'=\ln\hat{\beta}} = -\frac{\hat{\beta}^2}{\sqrt{2\pi}\sigma^3}\,. \tag{3}$$

Note that the derivative must be evaluated at $\beta' = \ln\hat{\beta}$ because the normal distribution is unimodal and the logarithm is a monotonic function, so the maximum of the likelihood function of the log-transformed parameter must occur at the same point where the normal distribution has a maximum probability ($\hat{\beta}$), also log-transformed. This also means that

$$\hat{\beta} = e^{\widehat{\beta'}}. \tag{4}$$

To estimate σ we simply need to substitute (4) and the numeric estimate of H' into eqn. (3):

$$-\frac{1}{\sqrt{2\pi}\sigma'^3} = -\frac{\hat{\beta}^2}{\sqrt{2\pi}\sigma^3} \quad , \tag{5}$$

which means that

$$\sigma = \left(e^{\widehat{\beta'}}\right)^{\frac{2}{3}}\sigma'. \tag{6}$$

With these new parameters we rescaled the variance-covariance matrix, and used the package tmvtnorm (Stefan and Manjunath 2015) to simulate new random parameters from a truncated multivariate normal distribution. Truncation at zero is required to avoid negative values of the parameters that need to be positive for biological reasons. Then, we ran 10,000 simulations for each species as invader with a different random sample of one, three, six and nine associated species. In each run, we quantified the mean phylogenetic distance and the strength of each coexistence mechanisms (relative non-linearity, storage effect and fluctuation independent niche differentiation) as specified in the measurement of coexistence mechanisms section in the main text. We conducted the same GLMM analysis to regress the contributions of each coexistence mechanism and the invasion growth rates on the mean phylogenetic distances and the number of associated species as fixed effects. We found that the best structure for random effects was the same that is reported in the main text, i.e., it included for each species the interaction between the mean phylogenetic distance and the number of associated species. The smallest ΔAIC for a model with simpler random effects had at least 300 units of difference.

As in the analyses were parameter uncertainty was not considered, there were different models in competition for all coexistence mechanisms: one in which the strength of the mechanisms depended only on the number of associated species and others in which the effect of the mean phylogenetic distance was included (Table S1.1). However, the model that did not include phylogenetic effects had a relatively higher support in comparison with the analysis presented in the main text, and even became the best model in two instances. The only exception was the storage effect, for which the model without phylogenetic distance could be safely discarded (Table S1.1). It is likely that the uncertainty about whether phylogenetic effects should be included in the best model arises from the high interspecific variation, as some species are more sensitive to the effects of mean phylogenetic distance. In contrast, the confidence bands of the boostrapped models were narrow and clearly indicate that the strength of the coexistence mechanisms change with mean phylogenetic distance (Figure S1.1), even in the presence of parameter uncertainty.

Because of Jensen’s inequality, the patterns observed in the models without uncertainty (i.e., using the average of the parameters) could have been different from those observed in the average of the models with uncertainty. This was not the case. Coexistence mechanisms showed the same responses regardless of whether parameter uncertainty is included or not (Figure S1.1): there was a positive relationship between the invasion growth rates, fluctuation-independent niche differentiation and the mean phylogenetic distance, but the opposite was true for the storage effect and relative non-linearity (Figure S1.1). However, the mean values for these fluctuation-dependent mechanisms remained very close to zero. The random effects were similar to those observed without parameter uncertainty (Figure S1.2). These patterns were stronger as more species are interacting, in line with the hypothesis and the findings in the main text. As in the main text, these results support our conclusions that close-related species are less likely to coexist and that the patterns found in pairwise comparisons may not remain valid in multispecies scenarios.

Table S1.1. ΔAIC values for the models that describe the effects of mean phylogenetic distance (D) and the number of associated species (A) on the strength of long-term population growth rate ($\bar{r}_i$), fluctuation-independent niche differences (FIND), relative non-linearity (RNL), storage effect (SE), and low-density environment-competition covariance (E-C Cov). In all cases the random-effects structure of the best model contained different A + D + A × D terms for each focal species. Models with ΔAIC = 0 were the models with the best support on the data.

Model	$\bar{r}_i$	FIND	RNL	SE	E-C Cov
Intercept only	12.39	12.46	8.59	***1.26***	6.03
A	**0.00**	***0.01***	***0.25***	2.35	**0.00**
D	11.73	11.49	10.51	**0.00**	7.43
A + D	***0.01***	**0.00**	***0.03***	***1.66***	***1.95***
A × D	3.71	4.25	**0.00**	7.49	3.64
A + A × D	2.12	***1.93***	***1.57***	***0.05***	***1.98***
D + A × D	5.53	6.13	***0.87***	***1.93***	3.44
A + D + A × D	***1.92***	***1.92***	***1.73***	2.04	3.81

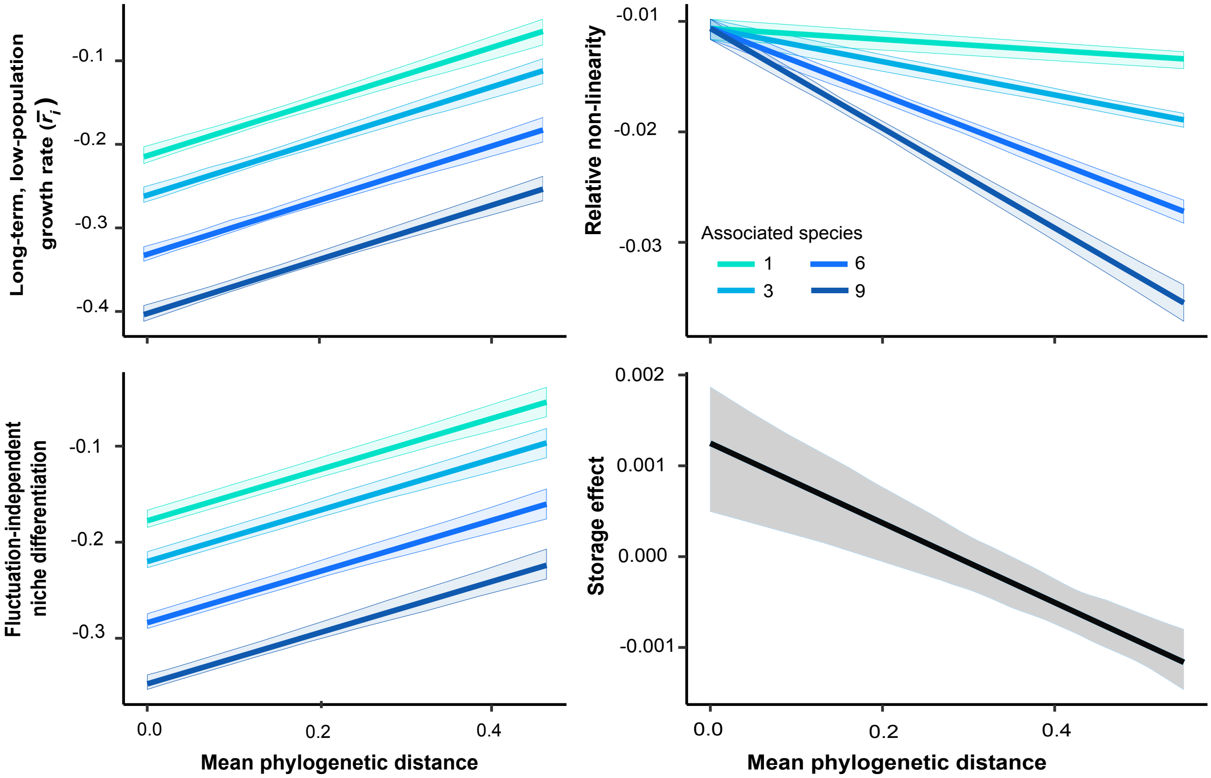

Figure S1.1. Relationship between phylogenetic distance and the long-term, low-density population growth rate, fluctuation independent niche differentiation, relative non-linearity and the storage effect. Ribbons correspond to 95% confidence intervals.

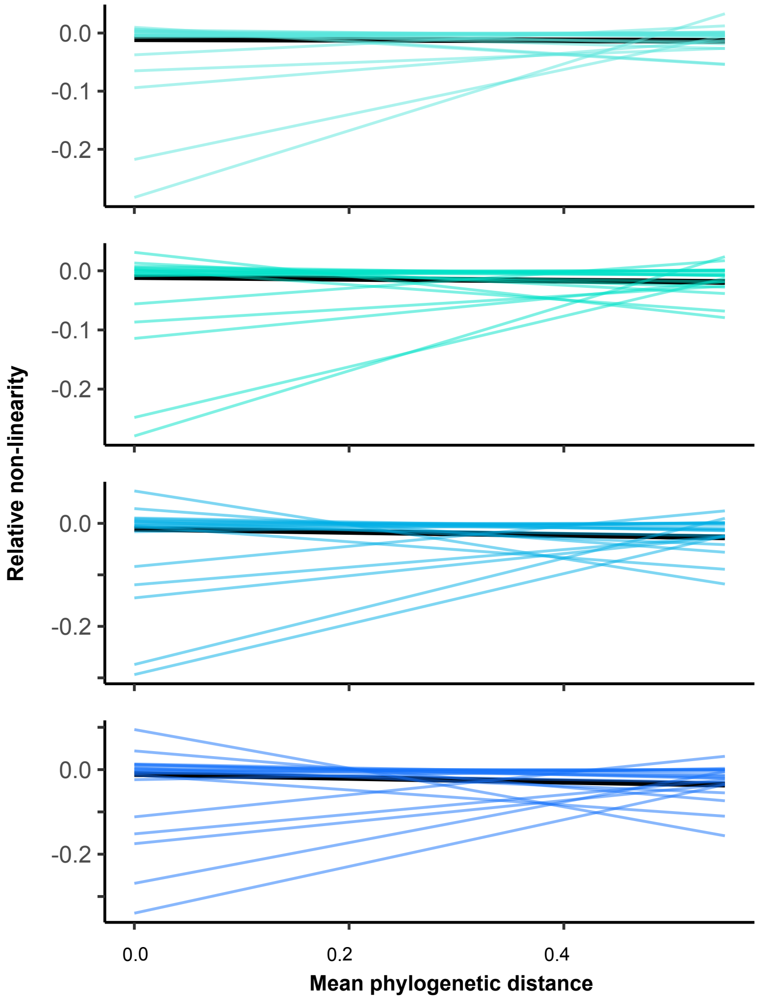

Figure S1.2. Relationships between the man phylogenetic distance and relative non-linearity for each study species depending on the number of associated species. The thick line shows the mean response.

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Online Appendix S2: Summaries of model statistics and figures

Table S2.1. ΔAIC values for the models that describe the effects of mean phylogenetic distance (D) and the number of associated species (A) on the strength of long-term population growth rate ($\bar{r}_i$), fluctuation-independent niche differences (FIND), relative non-linearity (RNL), storage effect (SE), and low-density environment-competition covariance (E-C Cov). Models with ΔAIC = 0 were the models with the best support on the data.

Invasion growth rate ($\bar{r}_i$)

Random Fixed	1	A	D	A + D	A + D + A × D
1	17920.8	4106.1	14949.1	479.8	13.1
A	9375.8	4089.1	6014.9	467.6	1.5
D	17111.3	3163.3	14945.8	481.5	14.0
A + D	8487.5	3146.4	6011.8	464.5	3.3
A × D	12764.4	3064.5	6918.5	361.7	9.5
A + A × D	8450.2	3031.2	5916.6	331.0	**0.0**
D + A × D	9347.1	3051.7	6903.1	362.9	11.4
A + D + A × D	8396.4	3021.7	5917.5	332.8	0.2

Fluctuation-independent niche differentiation (FIND)

Random Fixed	1	A	D	A + D	A + D + A × D
1	17934.7	3889.3	3889.3	409.6	12.9
A	9255.5	3872.4	6030.3	397.6	1.8
D	17104.5	2921.0	15086.3	411.1	14.0
A + D	8342.9	2904.0	6026.8	394.1	3.7
A × D	12741.3	2831.7	6995.5	297.8	10.6
A + A × D	8268.8	2798.3	5905.7	267.9	0.1
D + A × D	9263.5	2815.4	6979.3	299.4	12.5
A + D + A × D	8226.7	2785.7	5906.8	269.6	**0.0**

Relative non-linearity (RNL)

Random Fixed	1	A	D	A + D	A + D + A × D
1	26980.3	3457.5	23252.4	536.4	1.2
A	5619.5	3458.1	2776.0	536.5	1.9
D	5745.9	3412.8	2955.0	537.5	**0.0**
A + D	5576.7	3413.4	2777.6	538.0	0.2
A × D	5613.2	3431.8	2811.3	536.0	2.1
A + A × D	5610.2	3433.8	2757.5	533.0	3.9
D + A × D	5610.2	3412.5	2813.2	536.3	0.5
A + D + A × D	5558.7	3410.5	2757.9	533.9	2.2

Storage effect (SE)

Fixed \ Random	1	A	D	A + D	A + D + A × D
1	14197.3	5178.0	10469.4	944.6	4.1
A	12928.3	5176.9	9132.9	945.4	**0.0**
D	13840.8	4787.3	10469.1	946.2	1.9
A + D	12568.1	4786.3	9132.6	946.3	1.6
A × D	13379.9	4714.5	8991.6	907.3	0.4
A + A × D	12835.4	4704.2	8979.0	871.9	0.5
D + A × D	12431.1	4713.9	8987.8	882.4	2.1
A + D + A × D	12417.8	4704.8	8973.3	873.8	1.6

Low-density environment-competition (E-C) covariance

Fixed \ Random	1	A	D	A + D	A + D + A × D
1	11712.2	5260.5	5260.5	427.4	10.9
A	8341.8	5248.2	3665.3	421.9	3.4
D	10259.1	3708.3	7224.1	429.3	11.8
A + D	6845.5	3696.1	3660.3	416.9	3.1
A × D	10518.7	3691.4	4485.7	335.5	6.5
A + A × D	6231.5	3649.6	3039.3	300.6	4.8
D + A × D	7634.0	3610.0	4474.1	331.3	7.9
A + D + A × D	6233.1	3579.7	3041.2	301.0	**0.0**

Table S2.2 Estimated parameters for the fixed effects of the models for the long-term growth rate of the invader at low density ($\bar{r}_i$), storage effect (SE), relative no-linearity (RNL), fluctuation independent niche differentiation (FIND) and E-C covariance. D = mean phylogenetic distance and A = number of associated species. The number of observations for each model was 85,784.

		Estimate	Std. Error	t value
$\bar{r}_i$	Intercept	0.2483	0.0382	6.4930
	A	-0.0156	0.0037	-4.1740
	A × D	0.0150	0.0073	2.0460
SE	Intercept	-0.0002	0.0001	-1.8950
	A	-0.0001	0.0001	-1.6210
RNL	Intercept	0.0019	0.0006	3.2860
	D	-0.0032	0.0016	-1.9560
FIND	Intercept	0.2368	0.0396	5.9750
	D	0.0327	0.0221	1.4760
	A	-0.0159	0.0034	-4.6790
	A × D	0.0177	0.0069	2.5890
E-C covariance	Intercept	0.0056	0.0014	3.9040
	D	-0.0091	0.0032	-2.8640
	A	0.0015	0.0004	3.5930
	A × D	-0.0022	0.0009	-2.4130

Table S2.3 Summary statistics of the estimated random effects of the models for each coexistence mechanims and E-C covariance.

	Estimate	Std. Dev.
$\overline{r}_i$	Intercept	0.1698
	D	0.0893
	A	0.0166
	D × A	0.0340
	Residual	0.0771
SE	Intercept	0.0018
	D	0.0018
	A	0.0024
	D × A	0.0045
	Residual	0.0062
RNL	Intercept	0.0025
	D	0.0064
	A	0.0012
	D × A	0.0032
	Residual	0.0058
FIND	Intercept	0.1723
	D	0.0886
	A	0.0146
	D × A	0.0289
	Residual	0.0734
E-C covariance	Intercept	0.0061
	D	0.0130
	A	0.0017
	D × A	0.0038
	Residual	0.0099

Table S2.4 ΔAIC values for the models that describe the effects of mean phylogenetic distance (D) on the strength of competition coefficients ($\alpha_{i,j}$). Models with ΔAIC = 0 were the models with the best support on the data.

Competition ($\alpha_{i,j}$)

Random Fixed	1	D
1	18.23	5.38
D	3.22	**0.0**

Table S2.5 Estimated parameters for the fixed and random effects for the model that describes the effect of mean phylogenetic distance (D) on the strength of competition coefficients ($\alpha_{i,j}$). D = phylogenetic distance. The number of observations was 303.

		Estimate	Std. Error
Fixed effects	Intercept	0.0511	0.0095
	D	-0.0957	0.0231
Random effects	Intercept	-	0.0299
	D	-	0.0585
	Residual	-	0.0599

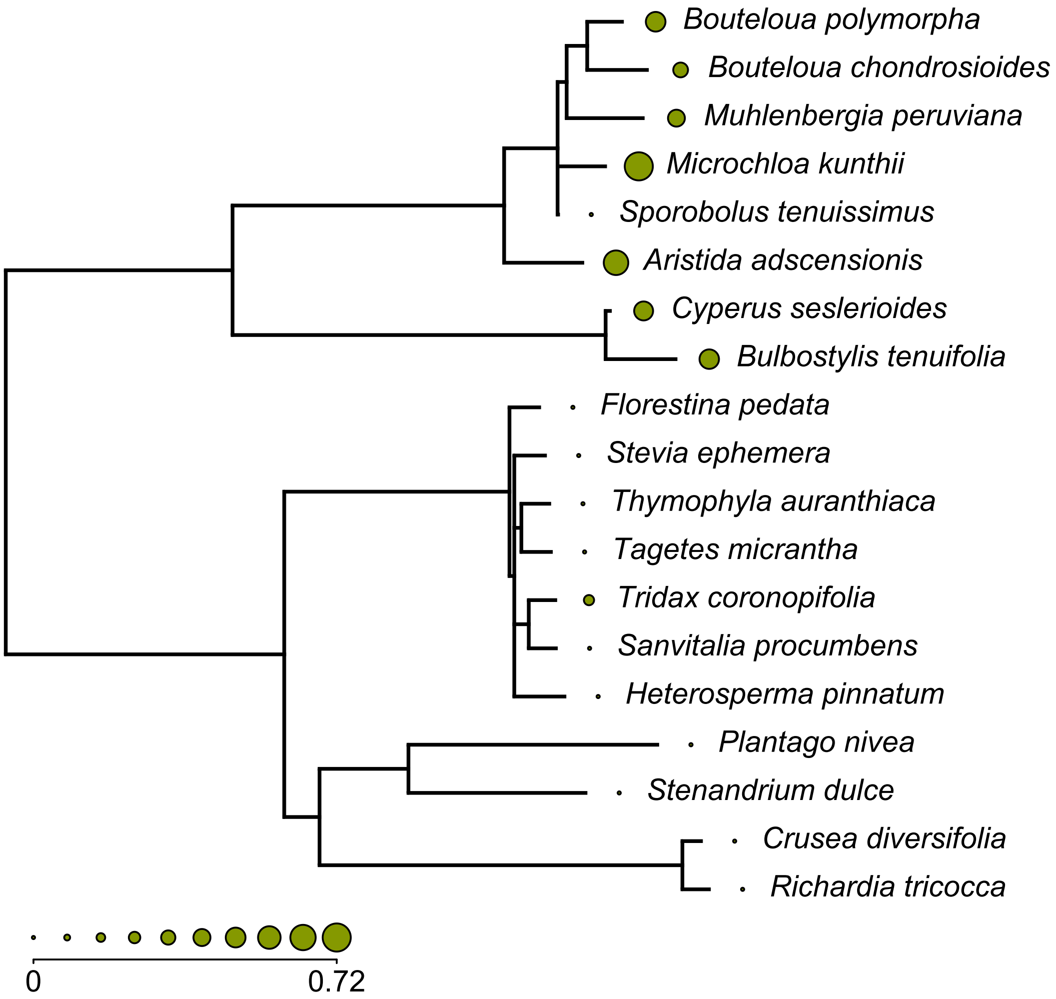

Fig. S2.1 Phylogenetic relationships and competition buffering responses (*b* values) of the study species. The amount of competition buffering is proportional to the size of the circles.

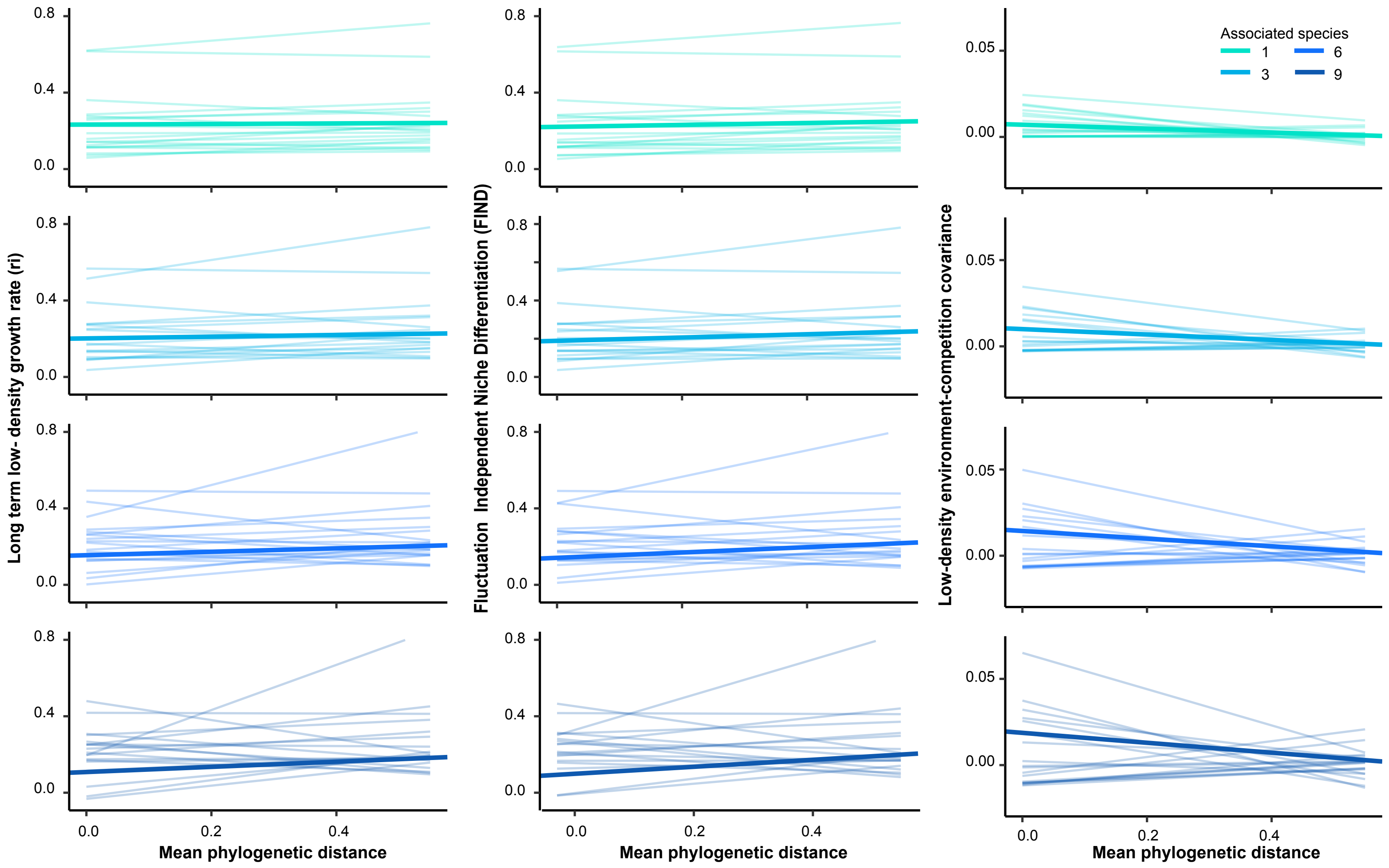

Fig. S2. 2 Relationship between the mean phylogenetic distance and the long-term, low density growth rate $\bar{r}_i$, fluctuation independent niche differentiation and low-density environment-competition covariance for each study species depending on the number of associated species. The thick line shows the mean response.

Online Appendix S3: Scatterplots for each study species

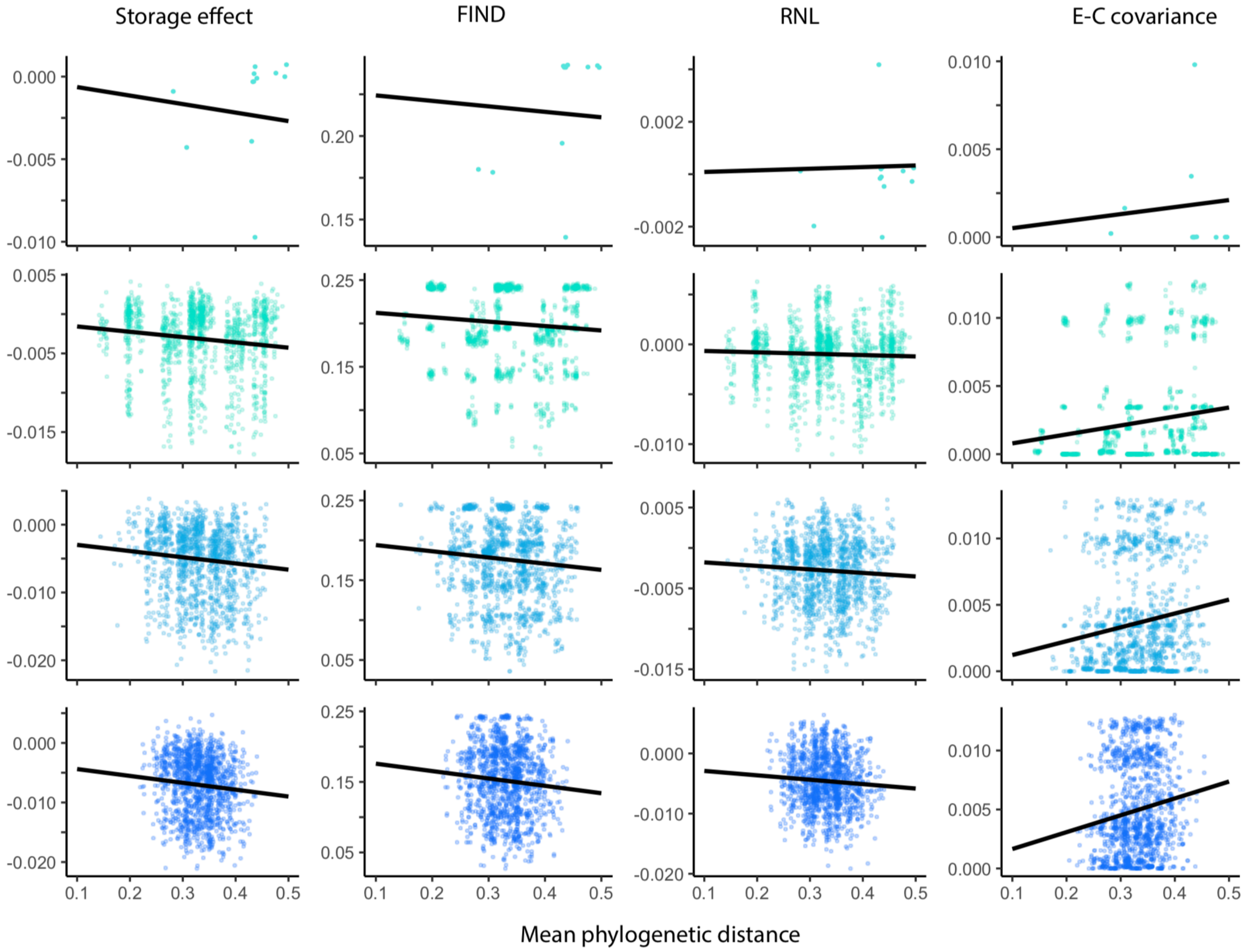

Fig. S3.1 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Aristida adscensionis* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

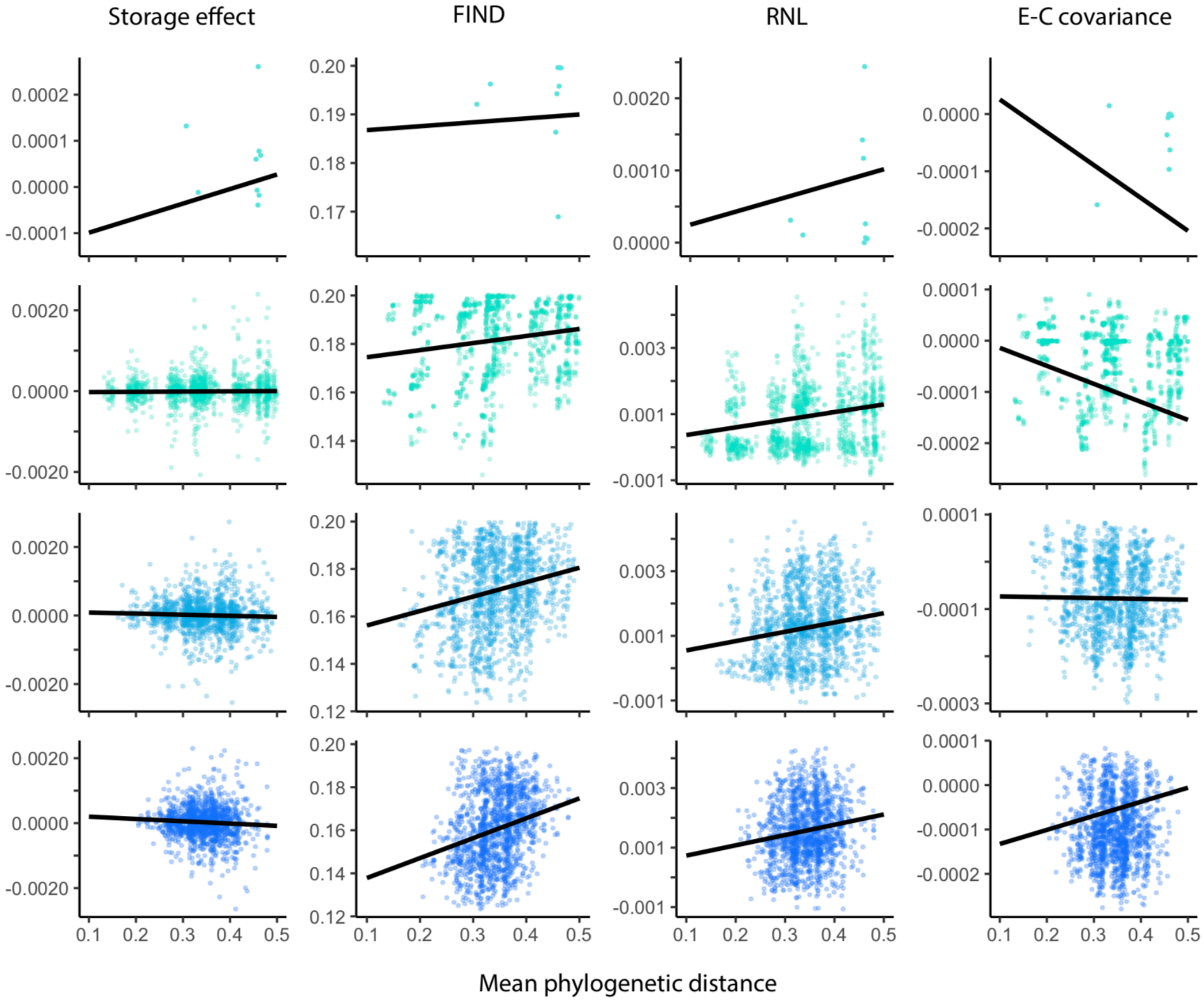

Fig. S3.2 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Bouteloua chondrosioides* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

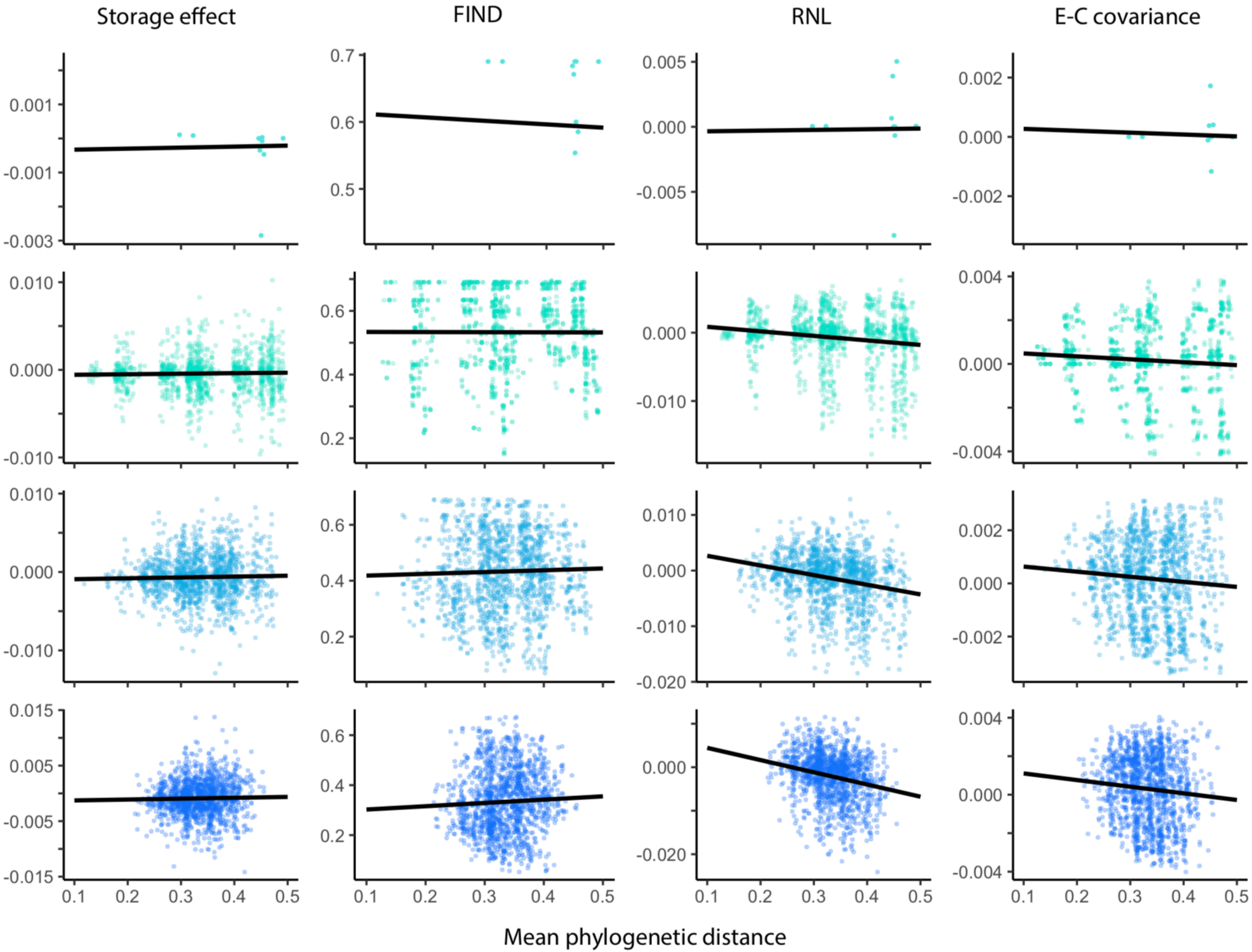

Fig. S3.3 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Bouteloua polymorpha* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

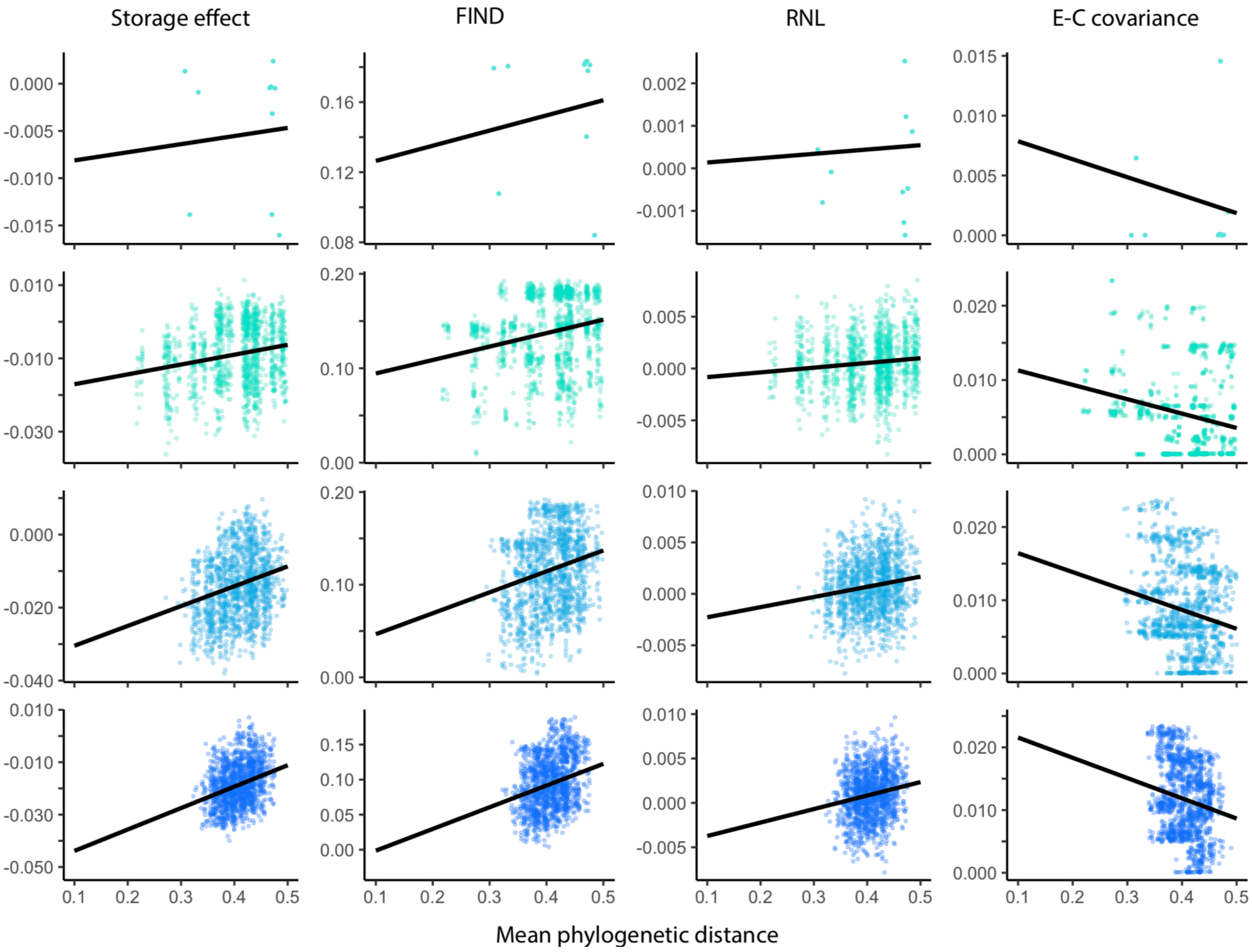

Fig. S3.4 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Bulbostylis tenuifolia* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

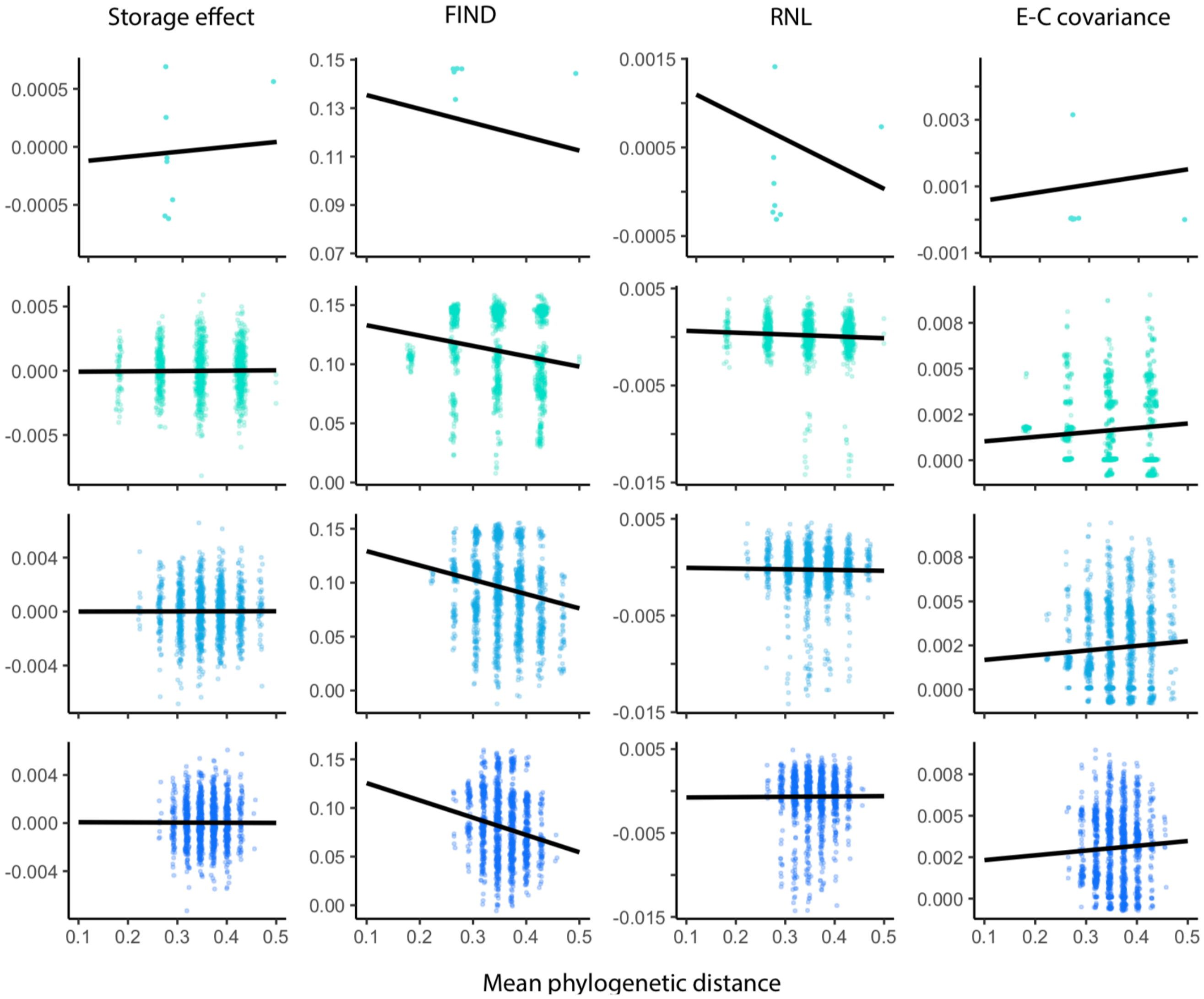

Fig. S3.5 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Crusea diversifolia* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

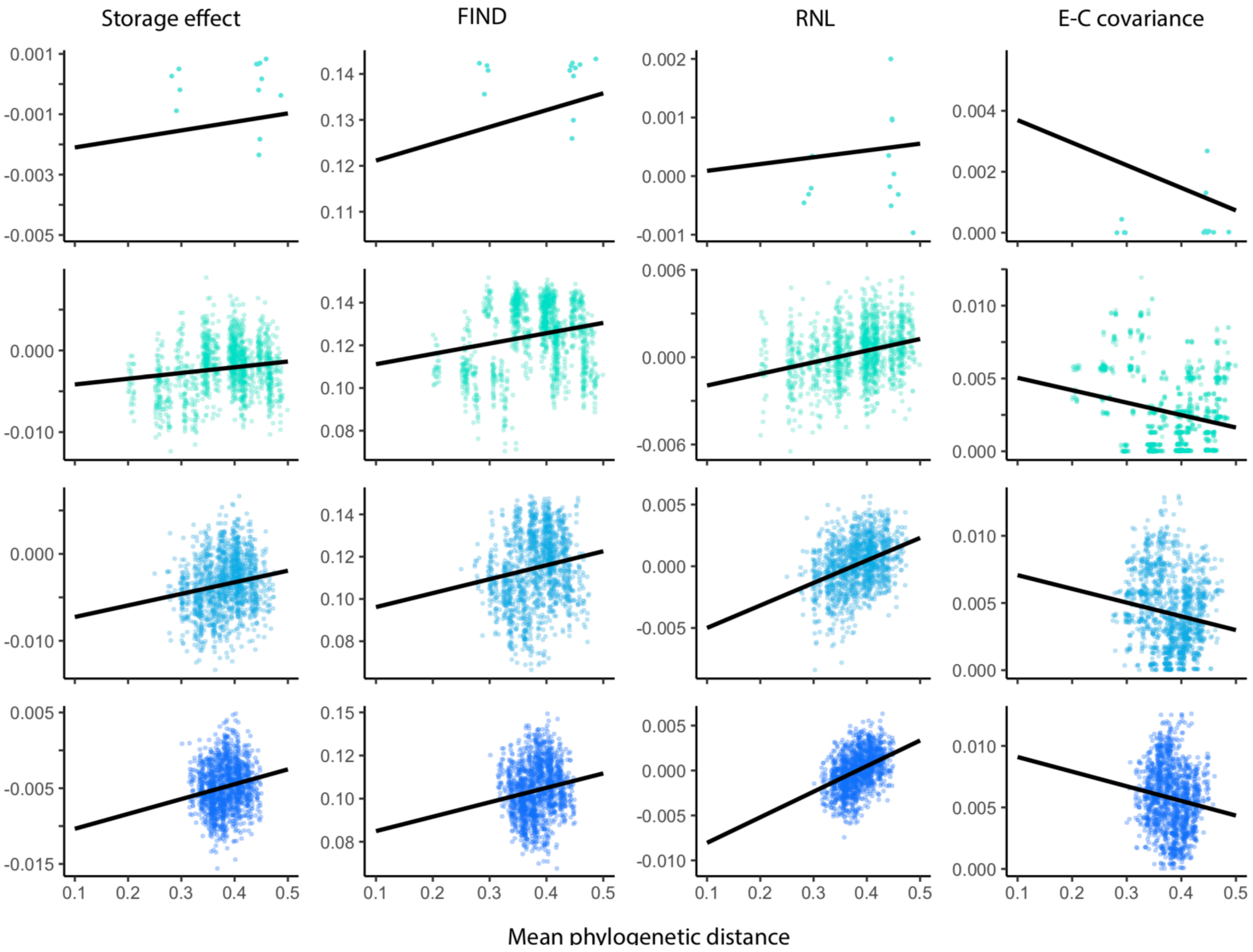

Fig. S3.6 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Cyperus seslerioides* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

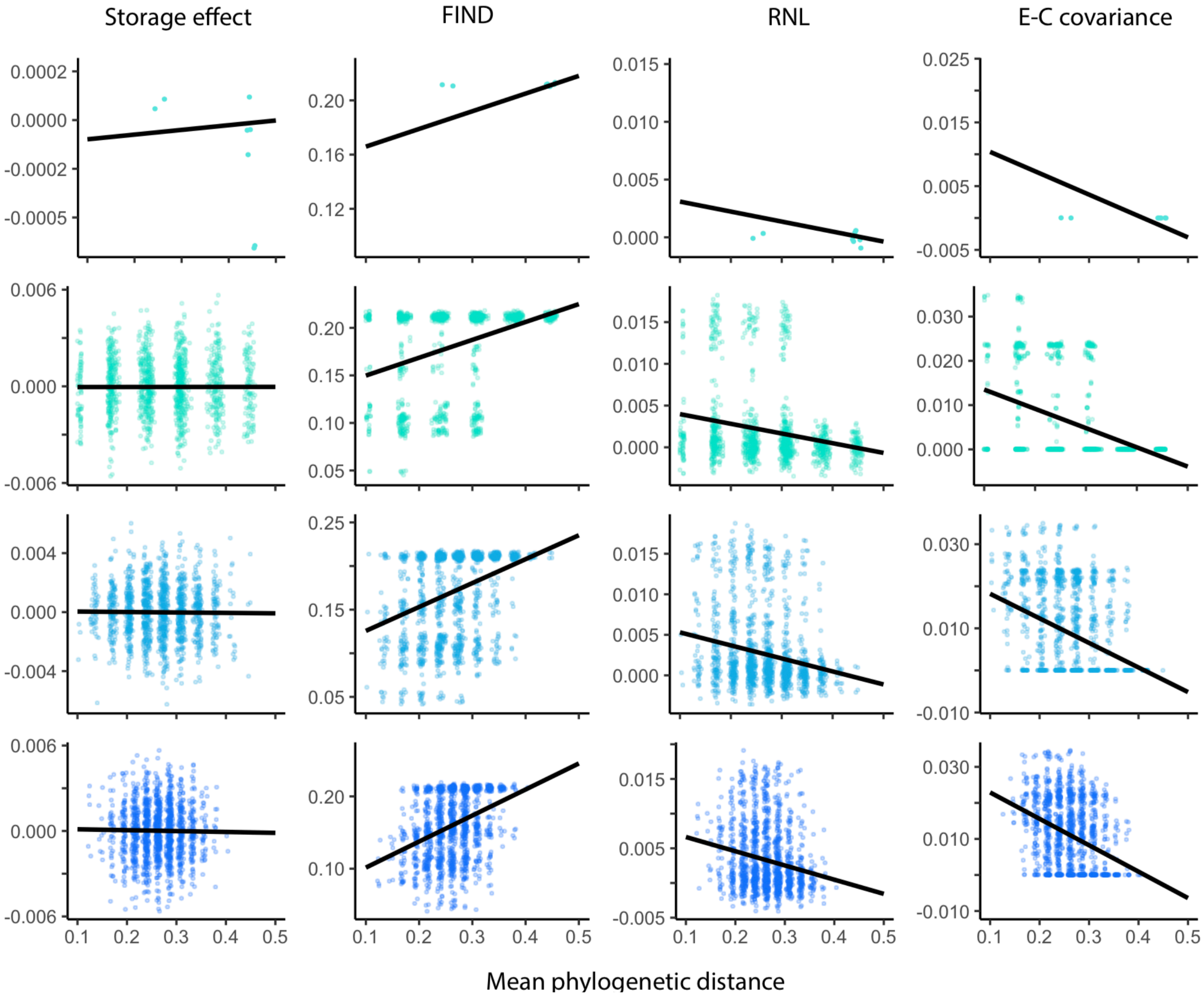

Fig. S3.7 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Florestina pedata* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

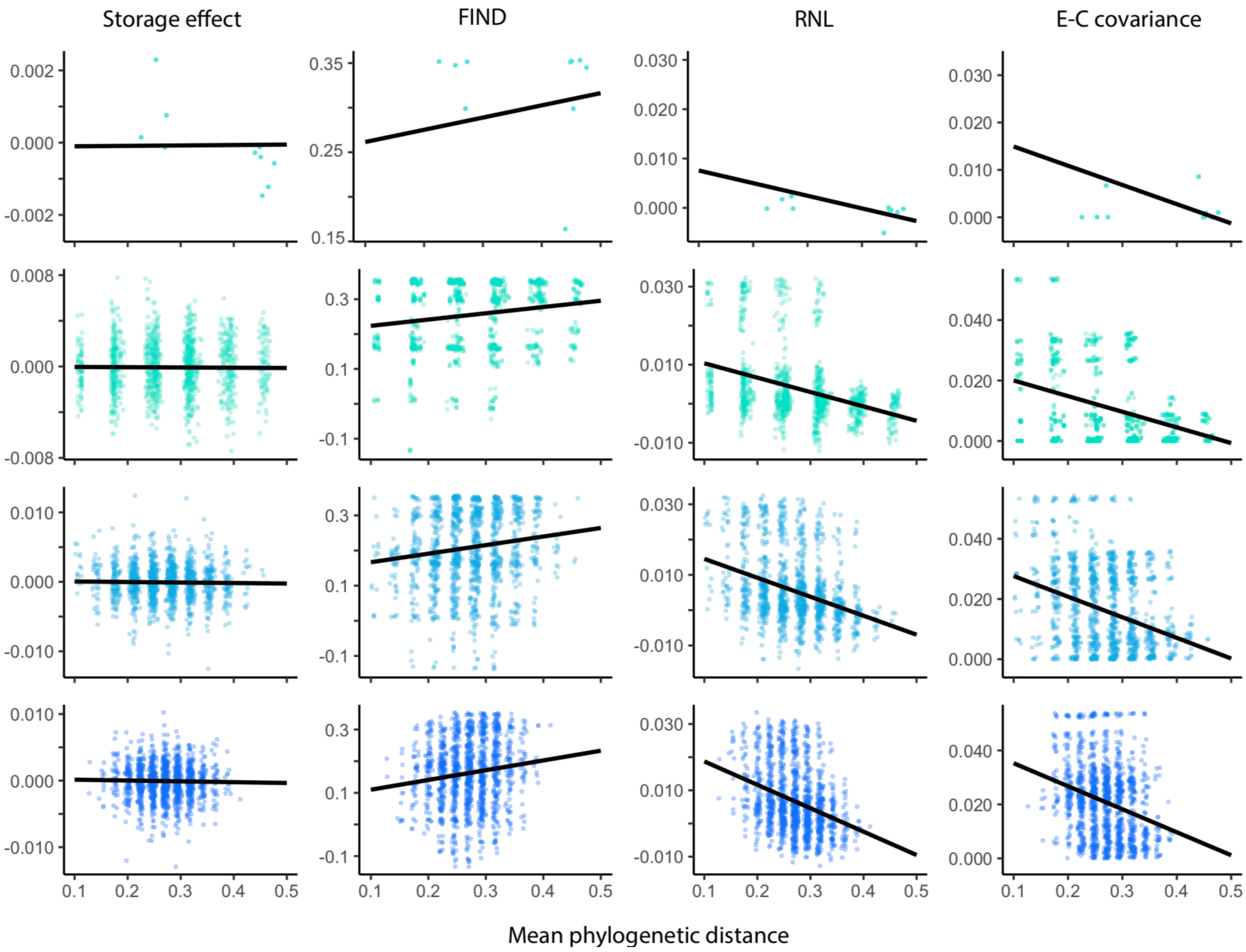

Fig. S3.8 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Heterosperma pinnatum* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

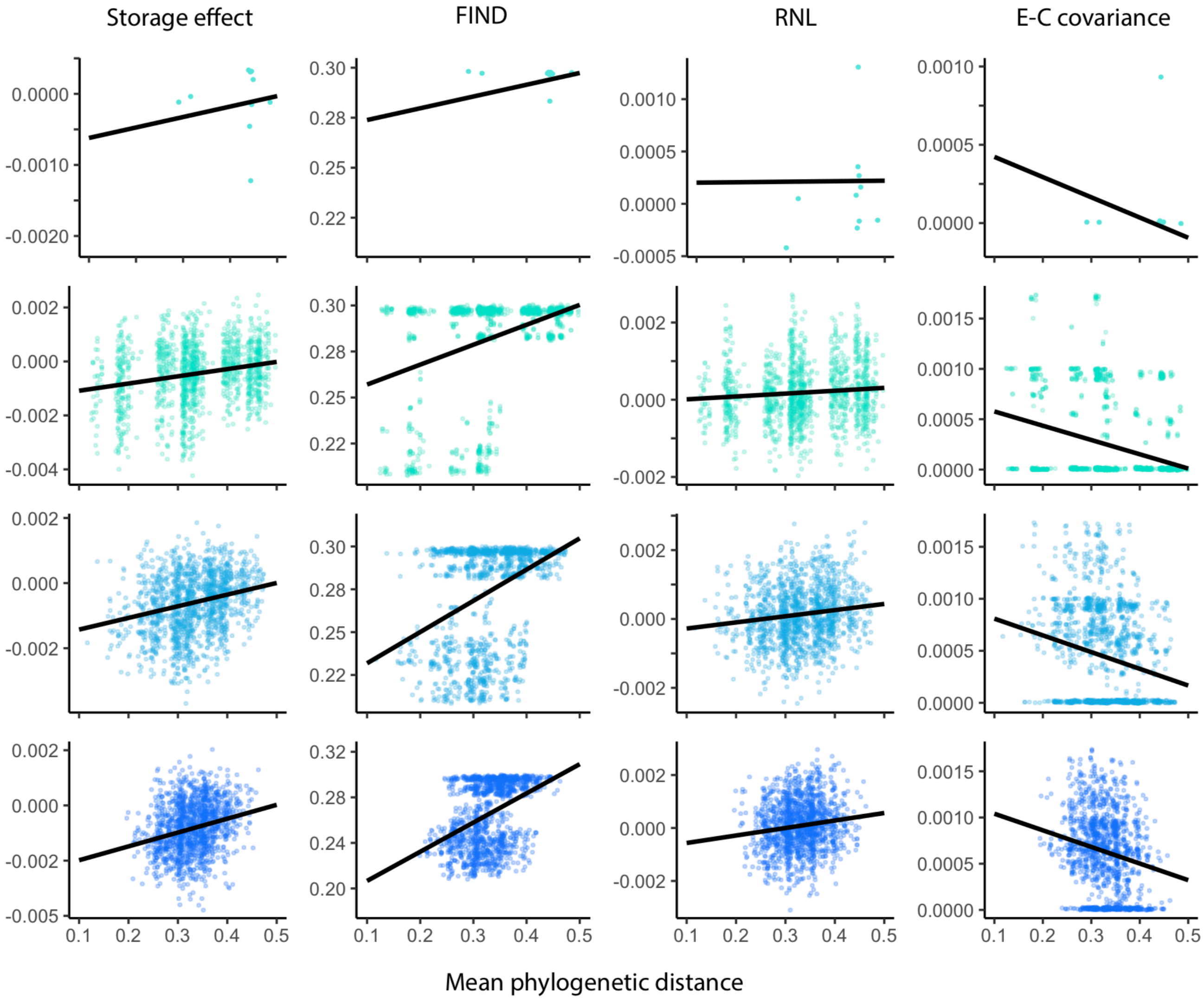

Fig. S3.9 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Microchloa kunthii* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

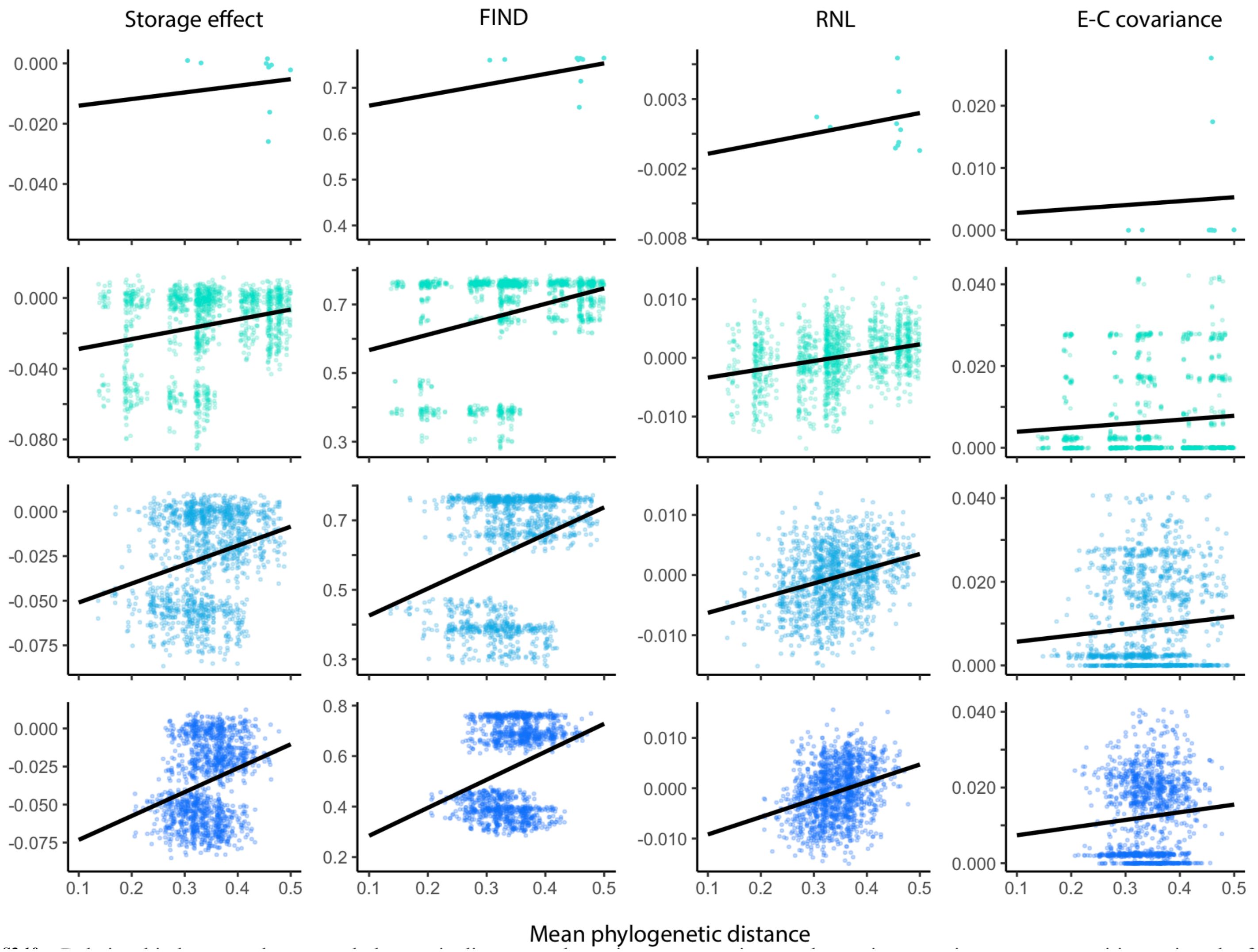

Fig. S3.10 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Muhlenbergia peruviana* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

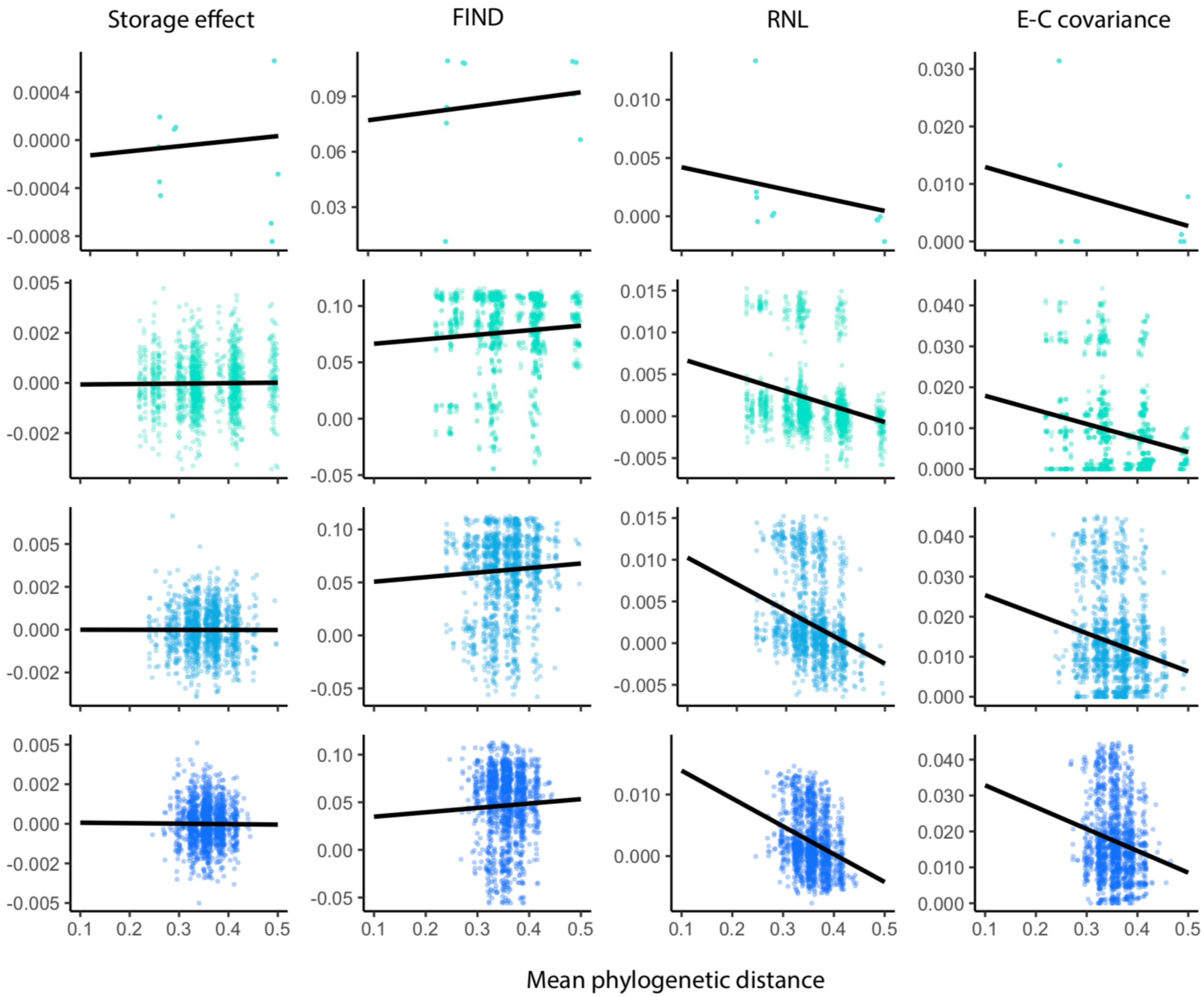

Fig. S3.11 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Plantago nivea* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

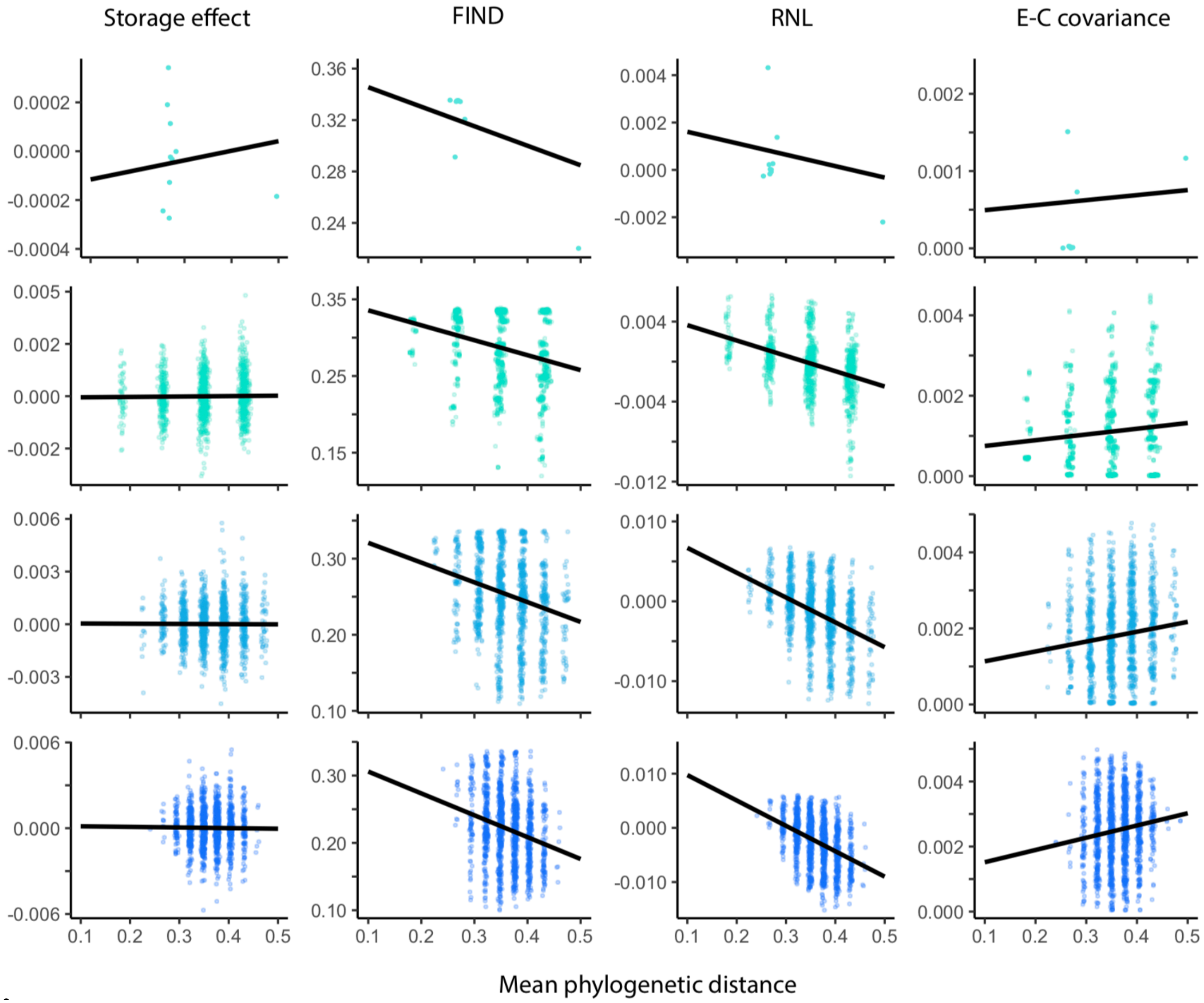

Fig. S3.12 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Richardia tricocca* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

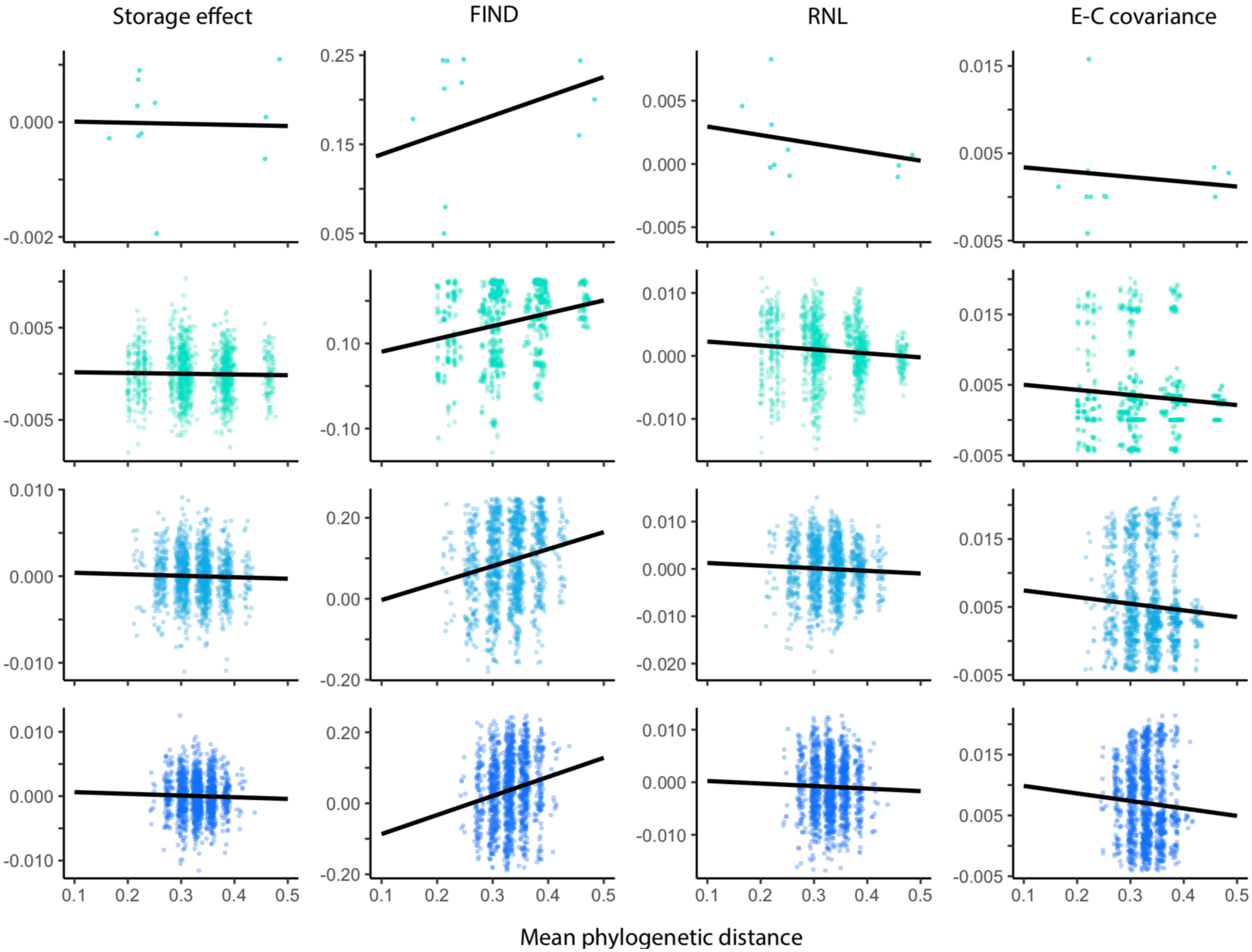

Fig. S3.13 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Stenandrium dulce* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

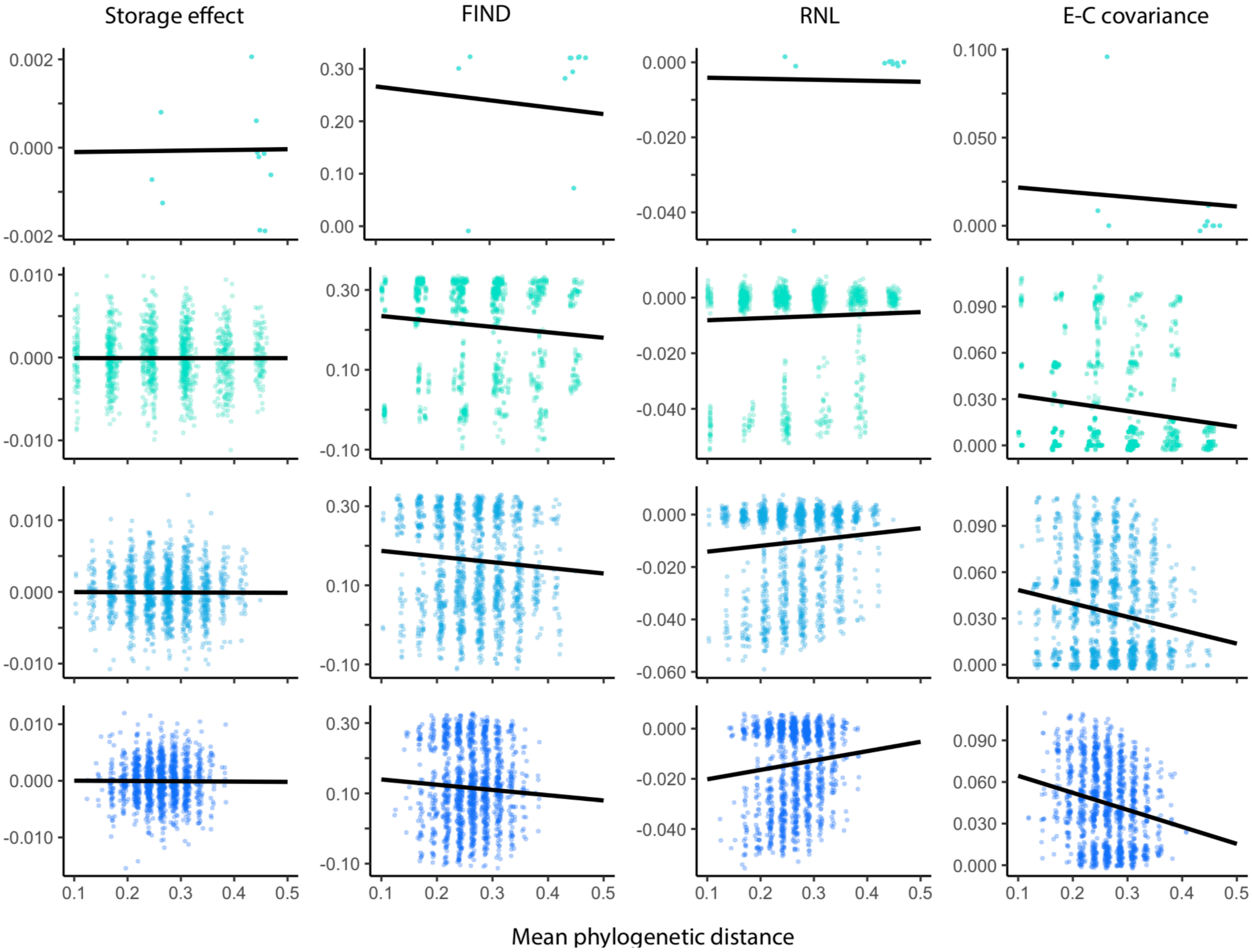

Fig. S3.14 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Stevia ephemera* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

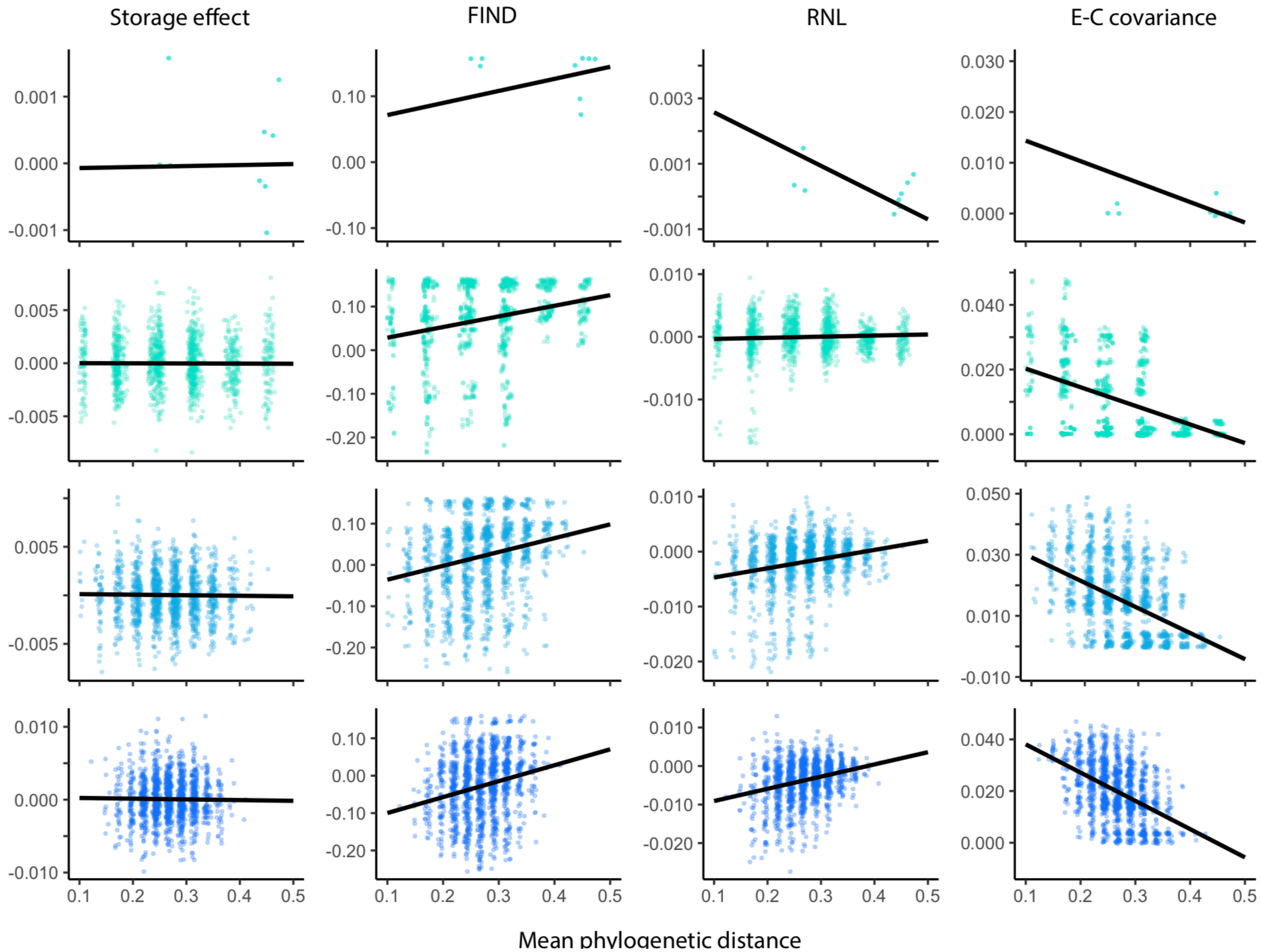

Fig. S3.15 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Sanvitalia procumbens* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

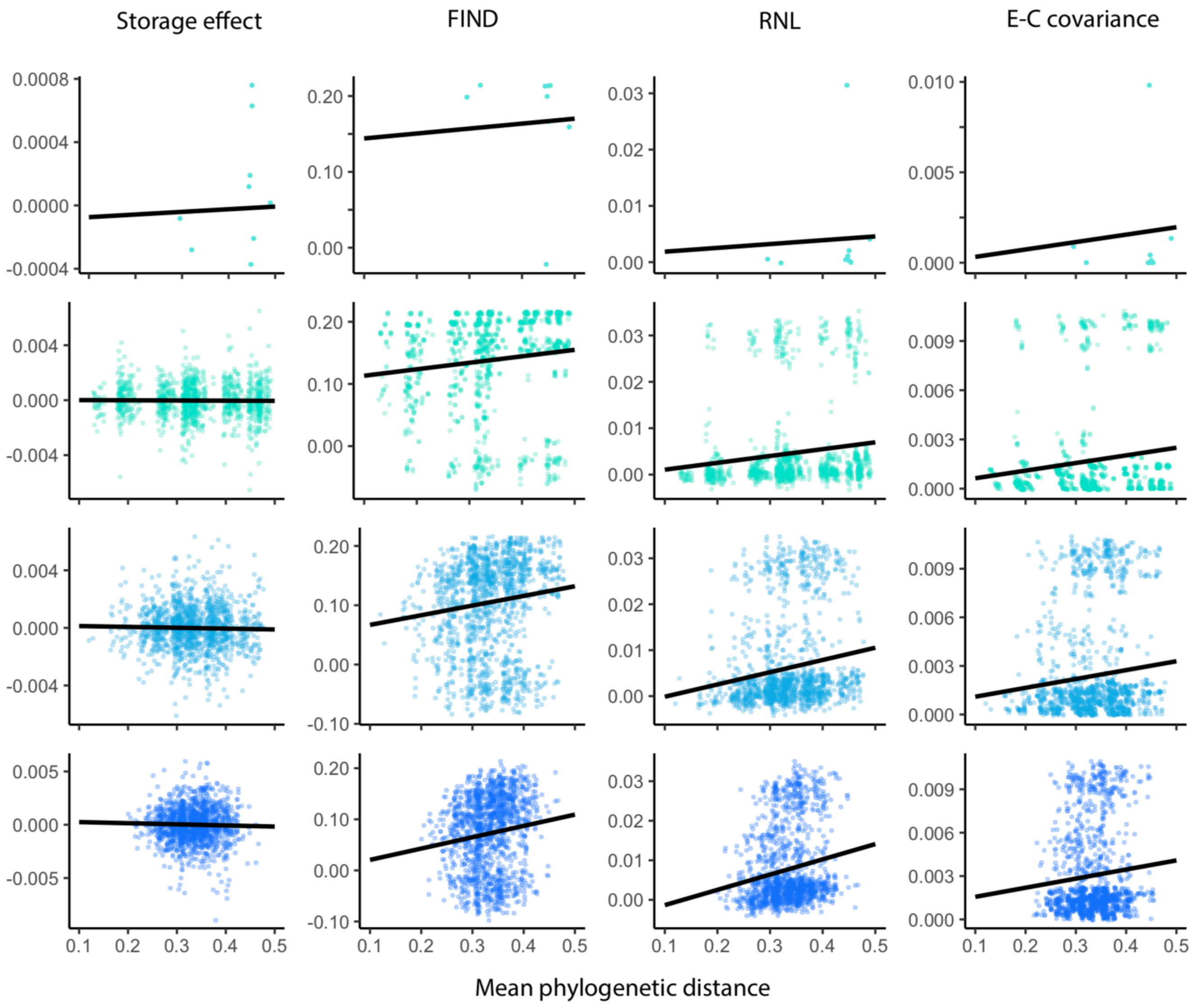

Fig. S3.16 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Sporobolus tenuissimus* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

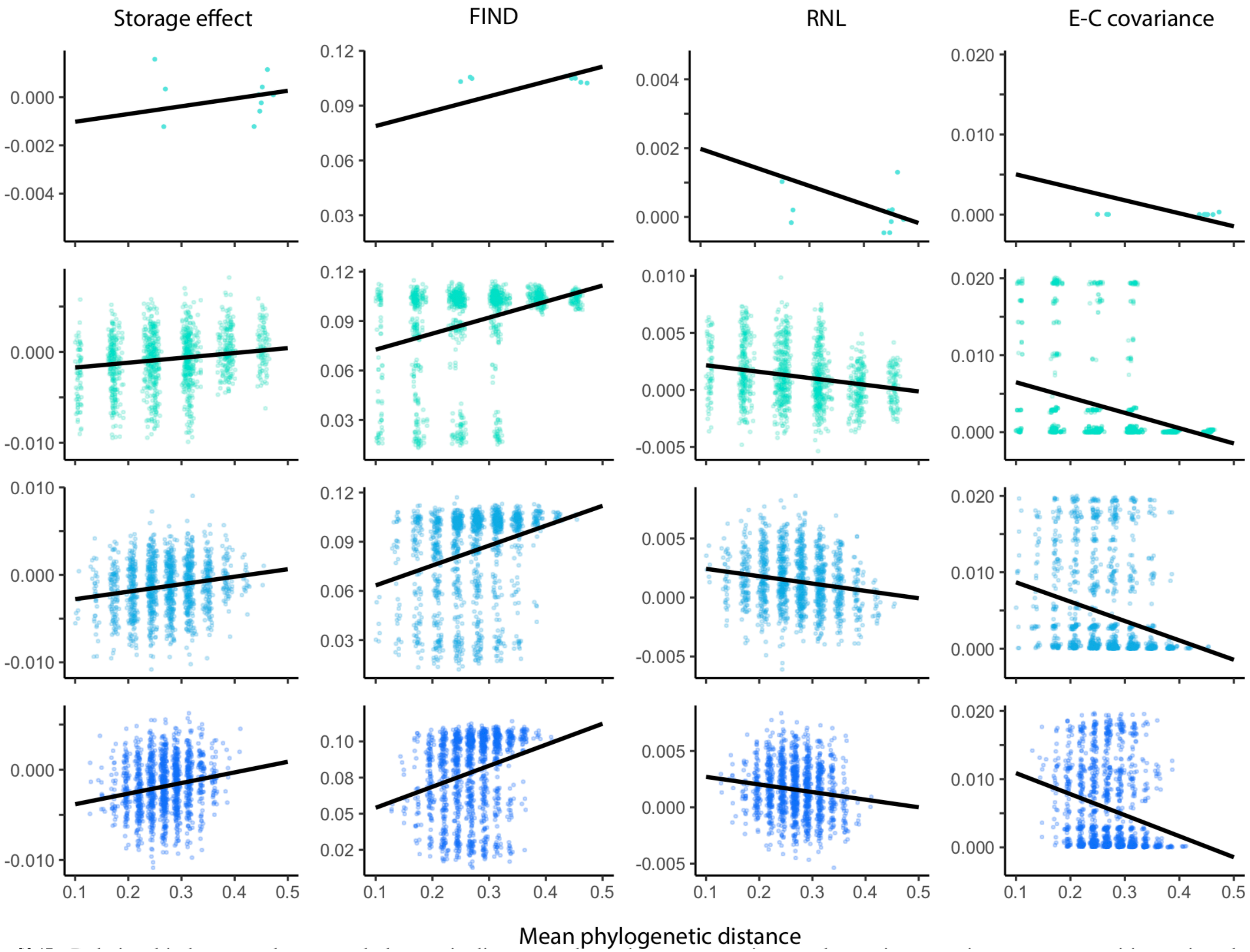

Fig. S3.17 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Tridax coronopifolia* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

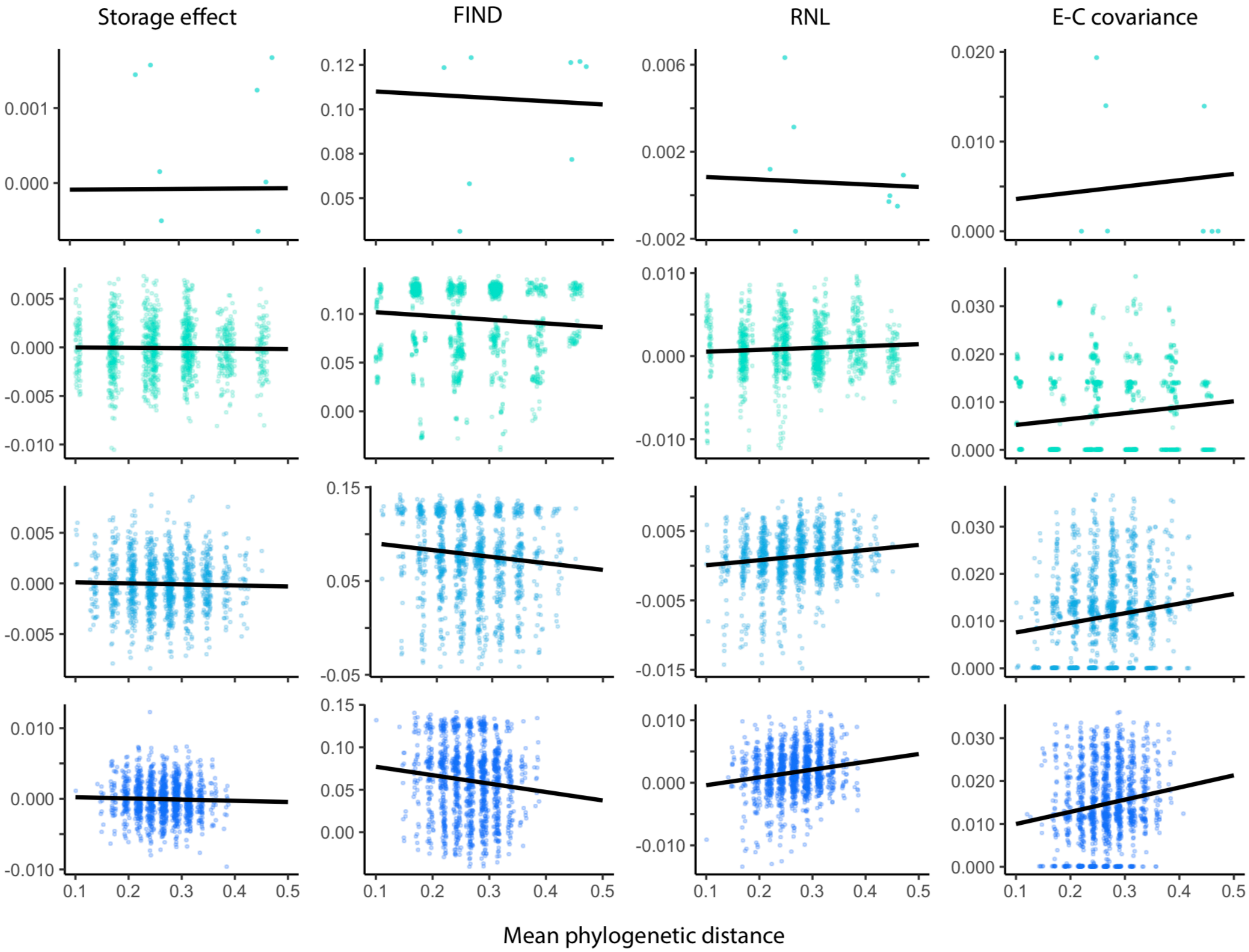

Fig. S3.18 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Tagetes micrantha* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Online Appendix S3: Scatterplots for each study species

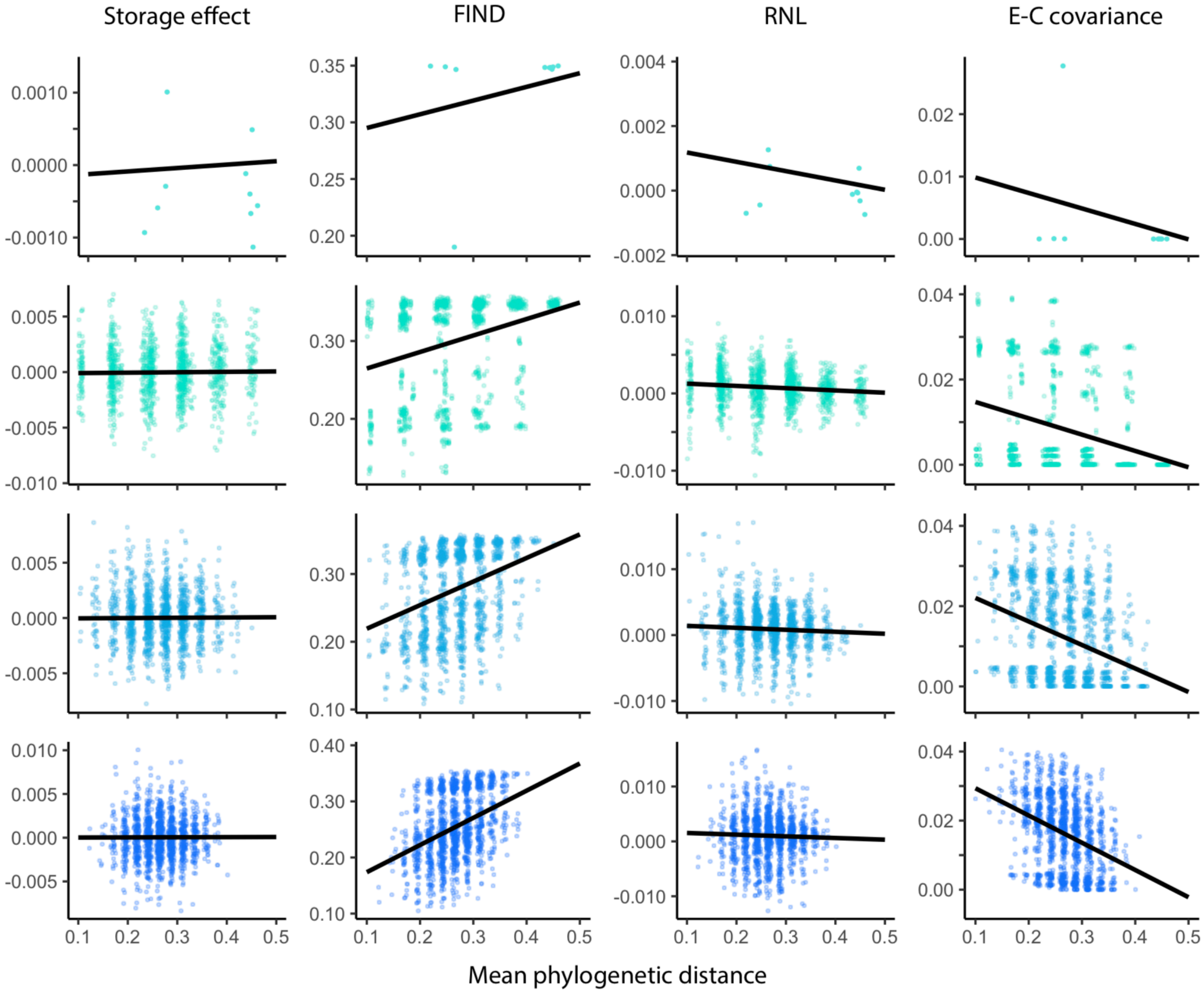

Fig. S3.19 Relationship between the mean phylogenetic distance and coexistence mechanisms and covariance environment-competition as invader for *Thymophyla auranthiaca* with one (first row), three (second row) and nine (fourth row) associated species. The thick line shows the mean response for this species.

Capítulo I I I

Mean life expectancy, but not seed banks, contributes to competition buffering in a semiarid grassland

V. Zepeda, E. J. González and C. Martorell. En preparación.

Mean life expectancy, but not seed banks, contributes to competition buffering in a semiarid grassland

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Keywords: Species coexistence, storage effect, species interactions, life-history traits, longevity.

Introduction

Models of species coexistence have shown that life history traits may be decisive for diversity maintenance in variable environments. These traits may act as buffers against adverse environmental conditions and competitive factors (Chesson & Huntly 1988). In modern coexistence theory this is called competition buffering, as the joint effects of environment and competition are less negative than the sum of their separate effects (i.e. there is subadditivy between the effect of environment and competition; (Chesson & Huntly 1988; Chesson 1994).

Competition buffering –one of the conditions for storage effect to promote stable coexistence– means that the effects of good times are "stored" to get populations through unfavourable years. This is supposed to occur when organisms have some stages in the life-cycle that are relative insensitive to the environment. For instance, a long-lived adult stage or dormant stages, like long-lived seed banks. However, empirical demonstrations of how different life history traits may help species to cope with unfavourable environmental conditions and the negative effects of competition are uncommon.

Seed banks have long been recognized as potential promoters of coexistence (Harper 1977). Theoretical studies have shown them to be crucial in fluctuating environments, which are highly unpredictable, as they increase the time to extinction (Kalisz & McPeek 1993). Species are likely to differ in their responses to environmental conditions (Pake & Venable 1995). Thus, unfavourable years for one species may be favourable for its competitors. Without seed survival from one year to the next in the seed bank, a species might go extinct (Chesson & Huntly 1988). But, dormant seeds may buffer competition as they are less affected by environmental factors and competition in comparison with the actively growing plants (Chesson *et al.* 2014). This is relevant when species is at low density as individuals are able to persist in the population and contribute later to population growth. The chances of buffer competition increase as seed survival and seed bank size increase.

Other stages in the life-cycle, such as the adults of iteroparous plants, can also buffer the combined effects of competition and adverse environmental conditions (Chesson 2003). Persistence of adults limits the damage from unfavourable conditions and favours strong growth at other times (Chesson *et al.* 2014). Long-lived species may store individuals that contribute to reproduction in different breeding seasons (Chesson & Huntly 1988). This increases the probability that a population can sustain positive average growth even when recruitment often fails provided strong recruitments in other times (Chesson & Huntly 1988). Thus, adult survival buffers population growth converting higher growth variance into higher mean growth (Chesson 1983). In contrast, short-lived species are expected to depend closely on high fecundity rates (García *et al.* 2008). As a result, they are more prone to local extinctions due to large temporal population fluctuations (Tuljapurkar & Orzack 1980; Menges 1997).

In this study, we test the hypothesis that seed banks and individual longevity buffer competition. If seeds and adults can survive to unfavourable conditions, they would contribute to maintain positive population growth rates by diminishing the negative effects of competition during the bad years. Later, they can contribute to population growth by germinating or reproducing in the following years. Thus, species with greater longevity, larger seed banks or high soil seed survival are expected to buffer competition more. To test this idea, we conducted a soil seed survival experiment in a semiarid grassland and took soil samples to characterize the seed bank of 19 species of forbs and grasses. To estimate mean life expectancy, survival and growth of nine perennial species were followed for five years. Then, we correlated these data with the capacity of species to buffer competition estimated in a previous work (Zepeda & Martorell 2019).

Methods

Our study was conducted in Concepción Buenavista, Oaxaca, Mexico. The climate is semiarid with a mean annual temperature of 16 ºC, and an annual rainfall of 530.3 mm (Martorell *et al.* 2017). The site is at 2275 m a.s.l. The vegetation is a short (<10 cm tall) grassland dominated by *Bouteloua* spp. (Cruz-Cisneros & Rzedowski 1980). Study species were the 19 most common species of the grassland, 11 are annual and 8 are perennial.

Soil seed bank composition

To assess changes in abundances in the soil seed bank over time, we conducted a repeated sampling on the same area over three years. We established the sampling sites (two plots of 50 × 100 m) in a representative area of the semiarid grassland. Samples were collected in 2013, 2014 and 2015 in winter (early December), after seed dispersal. In each site, samples were collected annually from 30 random points. A block of soil (5 cm × 5 cm × 3 cm deep) was excavated from each point and placed in a plastic bag. As spatial heterogeneity is high at the study site, the samples were taken from the same areas (~30 cm radius) every year to avoid any bias. Care was taken to sample a different portion of the soil every year. We mixed all the soil samples and removed visible tubers, roots and rhizomes. Then, the mixed soil sample was divided in two parts to assess soil seed banks composition by two germination trials in growth chambers at 25 ºC. The first trial was conducted just after the soil sample was taken. The second trial was conducted six months later as seeds might require time to mature. This is the time that seeds remain in the soil before germination season starts. Photoperiod was 12 h day^{-1}. Each tray was watered regularly during a month and a half to maintain a saturated condition. The soil was blended every two weeks to leave different parts of the soil exposed to light in order to increase germination probabilities. Each germinated seed was removed from the tray once it was identified at species level. This allowed us to determine the abundance of each study species in the soil and avoid double counting. Extracting seeds from the soil was not possible as most seeds at the study site are too small (some of them are smaller than 0.0644 mg).

Seed persistence

For seed banks to buffer competition, seeds must be viable for more than one year. A burial experiment was set up to determine the ability of 19 species to persist in the soil. Seeds were collected in two different years: November 2013 and November 2014, cleaned in the laboratory of all extraneous material, and placed in organza mesh bags (10 × 10 cm). Each bag was filled with 30-50 seeds. In total, 12 bags (around 600 seeds) with seeds from 2013 and 8 bags (around 400 seeds) from 2014 were buried for each study species. Each bag was buried in December 2013 along a 2 cm deep trench in the field site. Four randomly selected bags for each study species were retrieved in July 2014, 2015 and 2016, just before germination season starts. We kept 150 seeds of each species for initial tests. The experiment was conducted from December 2013 to December 2015. After retrieval, bags were taken directly to the laboratory and their contents were inspected. Seeds were carefully separated to assess their condition. They were placed in Petri dishes on 1% agar and incubated inside growth chambers at 25 ºC for three more weeks, and a photoperiod of 12 h day^{-1}. Seeds were counted as germinated when the tip of the radicle emerged. Non germinated seeds were placed in Petri dishes with ethephon 1-µmol/L (Baskin *et al.* 2003) to break dormancy and again they were incubated inside growth chambers at 25 ºC during three more weeks. Seeds that did not germinate after agar or ethephon treatment were cut or poked through the seed coat to determine viability. Seeds with juicy, oily, or fleshy embryos were considered as viable (Pake & Venable 1996). Testing viability using tetrazolium was not possible as most seeds were too small for location of stained embryos.

As we observed that most of the seeds remained in the soil surface and that they do not seem to be buried frequently, we conducted a seed survival experiment without burial. Six samples of 20-10 seeds from each study species were set on the soil from December 2014 to July 2015 surface during six months. This time interval corresponds to the time between the seed dispersal season and the seed germination season. After that time, we recovered the seed samples and repeated the same viability trials as in the seed burial experiment.

Plant survival

To estimate the mean life expectancy we followed the growth and survival of *140* individuals of the nine perennial study species for five years. Data were recorded every year, from November 2013 to November 2017. We measured the height and the number of leaves for *Plantago nivea* and *Bulbostylis tenuifolia* individuals, and calculated their size as the product of both variables. For the rest of the species, we measured two diameters and calculated their size as the area of an ellipse.

Competition buffering

To quantify the ability of species to buffer competition, we used a model that describes the population dynamics of the 19 study species published by Zepeda and Martorell (2019). This model was parameterized with field data that came from annual measurements of the number of individuals of every plant species in 4000 0.1 × 0.1 m quadrats over 13 years. The model for each focal species j was a modified version of the Hassell model where the intrinsic growth rates, $\lambda_{j,t}$, are allowed to vary every year t, the intra and interspecific competitive interactions are considered, and the exponent was modified to permit annual changes in the intensity of competition:

$$\frac{N_{j,t+1}}{N_{j,t}} = \frac{\lambda_{j,t}}{\left(1+\sum_{k}\alpha_{j,k}N_{t,k}\right)^{\exp(a_j+b_j\ln\lambda_{j,t})}}, \qquad \text{(Eq. 1)}$$

where $N_{j,t}$ is the abundance of species j at time t, $\lambda_{j,t}$,is the intrinsic growth rate of species j at time t, $\alpha_{j,k}$ is a per capita coefficient determining the competitive effect of species k on species j, and b_j determines the change in the exponent a_j as a result of environmental fluctuations. In the Hassell model the exponent is a constant, ω, but here it is a function of λ, which is a measure of how favourable or adverse a year is. This allows the model to be subadditive, this means that competition is able to change yearly as required by the storage effect (Chesson 1994). A positive value of b_j would increase the competition in favourable years and lessen the negative effects on unfavourable ones. Values of b_j close to zero mean that the species is not able to buffer competition. Subadditivity is thought to be the result of life-history traits such as seed banks or long-lived adults. In a previous study we showed that adult survival and seed banks affect the exponent of the Hassell model because ω decreases as seeds or established plants become more longevous (Zepeda & Martorell 2019). Models used to study the effects of fluctuations on coexistence usually assume that germination or longevity change from year to year (Chesson & Huntly 1988; Chesson 1994), so a fluctuating ω would be expected. Thus, eqn. (1) is a good option to represent a wide variety of life histories despite the fact that it does not explicitly incorporate their underlying attributes. Further details about the experimental design and model fitting are in Zepeda and Martorell (2019).

Analysis

For each species, seed bank size was quantified as the sum of all the germinated seeds in the trays with soil samples. We standardized seed abundance of each species with respect to the abundance of established plants. To do this, we used data from 16 randomly placed 1 × 1 m quadrats. In each quadrat there were 20 randomly chosen squares. Thus, 321 squares were sampled in late September-early October, which is when individuals are established, and in the reproductive stage. This census was performed in 2013, 2014 and 2015, which correspond to the same years in which soil samples were taken.

We calculated survival of seeds in the soil to determine if they were able to persist for more than one year, as required by the storage effect. Seed survival in the soil was measured as the ability of a seed to be viable after some period of time (18 or 30 months). Thus, survival probability was calculated as the sum of all the viable seeds (seed that germinated in agar, ethephon and with fresh embryos) divided by the total number of buried seeds. Because it was observed that not all the seeds get buried after they were released, we used the results of the seed survival experiment in the soil surface and in the soil to estimate survival. This procedure also allows incorporating the effect of other predators, e.g. ants. Given the difficulties of quantifying the probability of a seed to be covered by soil, we assumed that 25 % of the seeds get buried. Then, we estimated the probability that a seed remains viable in the seed bank after 18 months, which is the survival probability of a seed at the second year of being released, (P_S) as:

$$P_S = P_{buried} + P_{surface}, \qquad \text{(Eq. 2)}$$

where

$$P_{buried} = 0.25 P_{18\mathrm{b}},$$

$$P_{surface} = 0.75\, P_{6\mathrm{s}}\, (P_{18\mathrm{b}} / P_{6\mathrm{b}}),$$

P_{buried} is the seed survival probability after being buried for two growing seasons. $P_{surface}$ is the probability that a seed survives the first growing season in the soil surface and then the second growing season in the soil seed bank. $P_{18\mathrm{b}}$ is the seed survival probability after being buried for 18 months. $P_{6\mathrm{s}}$ is the seed survival probability after six months on the soil surface and $P_{6\mathrm{b}}$ is the seed survival probability after six months buried.

Mean life expectancy ($\bar{e}_j$) of the nine perennial species was calculated following Caswell (2001):

$$\bar{e}_j = \sum_{k=1}^{m} \mathrm{N}_{jk} , \qquad \text{(Eq. 3)}$$

where

$$\mathbf{N}_j = (\mathbf{I} - \mathbf{P}_j)^{-1}, \qquad \text{(Eq. 4)}$$

and $\mathbf{N}_j$ and $\mathbf{P}_j$ are the fundamental and transition matrices of species j, respectively, $\mathbf{I}$ is the identity matrix and m is the dimension of the matrices. The transition matrix corresponds to the discretized version of the transition kernel defined as

$$p(x_t,x_{t+1}) = s(x_t)g(x_t,x_{t+1}), \qquad \text{(Eq. 5)}$$

where $x_{t,}$ is the size at time t of an individual and $x_{t+1,}$ is the size at time $t+1$. p function was constructed from the fitted survival (s) and growth (g) models. To this, we adjusted generalized linear mixed effects models (GLMM) to the size and survival data using the lme4 package (Douglas et al. 2012) in R (R Core Team 2020) for each perennial species. These models were

$$\mathrm{logit}(s(x_t)) = \beta_0 + \beta_1 \ln(x_t) + u_i + v_{ij,} \text{ and} \qquad \text{(Eq. 6)}$$

$$g(x_t,x_{t+1}) = \frac{1}{\sigma_{\ln(x_{t+1})}\sqrt{2\pi}} e^{-\frac{(\ln(x_{t+1})-(\beta_0+\beta_1\ln(x_t)+u_i+v_{ij}))^2}{2\sigma^2_{\ln(x_{t+1})}}} , \qquad \text{(Eq. 7)}$$

where β_0 is the intercept, β_1 is the effect of $\ln(x_t)$, and u_i and v_{ij} are the random effects of the i-th plot and j-th quadrat on survival (Eq. 6) or growth (Eq. 7). Survival was assumed to follow a binomial distribution. We used a logit function for the survival and an identity function for growth.

To determine the role of soil seed survival, size of the seed bank or mean life expectancy of species and its ability to buffer competition, we performed a Bayesian regression between the log of the values of b_j, which is the measure of subadditivity, against the values of each of the variables. Those regressions were performed with the brms package in R (Bürkner 2017, 2018). Because data are not independent due to their phylogenetic relatedness, we incorporated the this relatedness as a random effect. To this end, we used the variance-covariance matrix of the phylogenetic distances between species to define the structure of the random error. We tried two different structures for the random effect: 1) where the fitted models for each species differed only in the intercept and, 2) where the intercept and the slope change with each of the different explanatory variables. Additionally, we performed a null model in which $\log(b_j)$ was a function of the intercept only. For each model, we computed the widely-applicable information criterion (WAIC) for each of the models and selected the one with the smallest value (Watanabe 2010). Then, we used the method by Gelman *et al.* (2019) to obtain a measure of the variance explained by each of the models.

Results

We found that 15 out of the 19 study species were viable after 18 or 30 months in the soil (Table 1). But, most of the species had relatively low survival rates (range 0-0.58) and grasses were the group with the smallest ones (with the exception of *S. tenuissimuss*). The size of the seed banks was very variable among years and species (SD = 8.91 ind) and also mean life expectancy (SD = 3.19 years).

For all the explanatory variables, the best model was the one in which the random effect of phylogenetic distance affects the intercept and the slope (Table 2). As expected, the longevity of the individuals helps to buffer competition (Fig.1). The model with the smallest ΔWAIC showed a positive relationship between the mean life expectancy and the log(*b*) (Table 2). Models of seed survival in the soil had better support than the null model, suggesting that seed survival is explaining some of the variance of the log(*b*) but their effects were very weak. In fact, explained variance of the models was relatively good (Fig. 1, see R^2 distributions in Appendix 1). However, the confidence intervals of all the explanatory variables always includes zero (Fig. 2).

Discussion

In this study we assessed the relationship between the size of the seed bank, soil seed survival, mean life expectancy and the potential of species to buffer competition. Evidence showed that mean life expectancy explained subadditivity, but no seed banks. These results highlight the importance of determining what specific features of the species traits are related with the ability of species to buffer population growth against the negative effects of unfavourable environmental and competitive conditions to better understand how storage effect may promote or preclude stable coexistence.

Longevity has been claimed as an important life history trait for the persistence of populations at harsh or extreme environments or under frequent long periods of adverse conditions (Eriksson 1996; Larson *et al.* 1999; García & Zamora 2003; Forbis & Doak 2004; von Arx *et al.* 2006; García *et al.* 2008). As expected, our results are in line with previous studies as we found that species with the highest mean life expectancies were the species with the highest values of subadditivity. This may suggest that living longer may be an adaptive strategy to persist in difficult ecological scenarios (García *et al.* 2008).

Longer-lived species have been found to be less sensitive to environmental variability in all vital rates, but especially in survival (Morris *et al.* 2008). For a species to be long-lived, survival rates are expected to be high and, as a consequence, the variance of that rates is expected to be small (Morris & Doak 2004; Morris *et al.* 2008). In plants, survival rates are often positively related with size (Harper 1977). In this study most of the species had the same tendency, with the sole exception of *Plantago nivea*. Larger individuals have higher survival probabilities and they are less affected by competition. For instance, at the study site, seedlings are likely to be largely affected by hydric stress whereas adults or large individuals are likely to survive those conditions (Martínez-López *et al.* 2020**).** Thus, long-lived individuals may be able to ameliorate the effects of dry years on population growth rates, even if all new recruits died, contributing to species persistence in the community. Moreover, the persistence under poor conditions of biomass for photosynthesis buffers these hostile conditions (Chapin *et al.* 1990).

Soil seed banks are a dynamic part of plant populations with a set of factors that quantitatively influence their entry, persistence and exit, all of which vary according to plant biology, time and their environment (Saatkamp *et al.* 2014). In this study, most of the species had persistent seed banks, as seeds were able to be viable after one year. However, grasses had transient seed banks or very low survival probabilities after one year. According to modern coexistence theory, seeds are required to be viable after one year for storage effect to operate (Chesson & Huntly 1988; Pake & Venable 1996). While this is a necessary condition, it is not sufficient as seeds also must show high survival when dormant and low germination rates in the field in order to successfully buffer population growth (Li & Chesson 2018). In this way, only a small fraction of the population will be affected by poor environmental conditions and competition (Chesson *et al.* 2014). As a consequence, the effects of competition on population growth are limited.

Annual Asteraceae had low seed survival probabilities ($\text{mean}_{18\ \text{months}} = 0.21 \pm 0.09$, $\text{mean}_{30\ \text{months}} = 0.13 \pm 0.11$) and relatively small seed banks. Which might make them more vulnerable to environmental variations as seed banks may not be reliable for their persistence. A full understanding of the significance of delayed germination and soil seed banks for species coexistence requires quantifying other processes associated with dormancy (Gremer *et al.* 2012). For instance seed predation, disease and damage can reduce the benefits of delayed germination (Ellner 1985; Donohue *et al.* 2010; Dalling *et al.* 2011). At the study site, granivory by ants determines plant population dynamics to a large degree (García ‐ Meza *et al.* 2020). Thus, delayed germination may not be a good strategy. Plasticity in germination responses has been suggested to be an alternative to bet-hedging in variable environments (Simons 2011). Species may bet for high fecundity and high establishment rates to persist in the community. Another option is predictive germination, which is the tendency to germinate when conditions will be favourable to growth, and not germinate when conditions are unfavourable (Gremer *et al.* 2016).

The potential of species to buffer competition diminished with seed soil survival. This suggests that the longevity of the seeds in the soil hindered the ability of the species to ameliorate the negative effects of competition and unfavourable periods. Age structure in seed banks may determine their contribution to population growth rates and, as a consequence, to diversity maintenance (Kalisz & McPeek 1992; Fenner & Thompson 2005). In spite of delayed germination is supposed to be a viable evolutionary and a demographic strategy to cope with environmental variability, intra-annual delay may reduce germination and establishment rates, which might reduce competitive ability (Long *et al.* 2009). This may explain why we found a negative relationship between seed soil survival and subadditivity. Age structure in seed banks has been reported to be analogous to extended juvenile stage in other organisms (Kalisz 1991), resulting in the late reproduction of longest-lived seeds, and negatively affecting the intrinsic growth rates (Cole 1954; Harper & White 1974; Sarukhan & Gadgil 1974). For instance, in agricultural species, the time required for germination and emergence of plants from aged seeds is greater than in fresh seed (Takayanagi & Harrington 1971). This delay is thought to reflect the time required for internal repair of damaged membranes that can only occur after the seed imbibes water (Berjak & Villiers 1972). As a consequence, the plant suffers both, a temporal delay in emergence and a potentially costly reallocation of internal resources (Rice & Dyer 2001). At population level, seed banks may also retard population growth in favourable years because dormant seeds delay reproduction (Lewontin 1965). However, our results showed that the log of *b* values decreases slightly with seed soil survival (Fig. 2), casting doubts on how important is this variable to competition buffering. In fact, we observed weak effects in all the explanatory variables, even when R^2 s were relatively high (Fig. 1). This suggest that most of the variance is explained by evolutionary relatedness of the species.

Our results highlight the importance of formally assessing the mechanisms that underlie competition buffering since most examples are anecdotal, with strong empirical tests being the exception (Simons 2011). In many studies, the presence of a resistant life stage has been presented as evidence for storage effects. However, the occurrence life stage may not always be responsible for competition buffering, as was the case of seed banks in our study. Moreover, the presence of a resting life stage may also be associated with other coexistence mechanisms. For instance, theoretical studies have shown that seed dormancy increases the nonlinearity of the relationship between the growth rate and competition (Kortessis & Chesson 2019). Species with dormant seeds seem to benefit more from variation in competition as they exhibit a convex response to competition than non-dormant ones (Kortessis & Chesson 2019). Furthermore, differences in the longevity of the species may also promote species coexistence by relative nonlinearity. Longer-lived species with high sensitivities to environmental variation may destabilize coexistence (Yuan & Chesson 2015). However, no empirical evidence is available. Thus, our study calls for a more serious life-history based approach to studying species coexistence.

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Table 1. Values of parameter *b*, size of the seed bank (number of germinated seeds in the tray) in each of the years of sampling, seed survival (number of viable seeds) after 18 and 30 months buried and mean life expectancy of the study species.

Species	Family	b_j	Size bank 2013	Size bank 2014	Size bank 2015	Seed survival 18	Seed survival 30	Mean life expectancy
Stenandrium dulce	Acanthaceae	0.00	0.00	0.00	0.00	0.00	0.00	NA
Heterosperma pinnatum	Asteraceae	0.00	13.00	26.00	15.00	0.19	0.15	0.00
Florestina pedata	Asteraceae	0.00	10.00	0.00	5.00	0.41	0.33	0.00
Sanvitalia procumbens	Asteraceae	0.00	0.00	0.00	0.00	0.13	0.10	0.00
Stevia ephemera	Asteraceae	0.00	56.00	50.00	41.00	0.14	0.00	0.00
Thymophyla auranthiaca	Asteraceae	0.00	52.00	9.00	53.00	0.19	0.13	0.00
Tagetes micrantha	Asteraceae	0.00	49.00	38.00	8.00	0.19	0.14	0.00
Tridax coronopifolia	Asteraceae	0.20	5.00	3.00	3.00	0.23	0.09	NA
Cyperus seslerioides	Cyperaceae	0.46	4.00	2.00	43.00	0.31	0.50	8.35
Bulbostylis tenuifolia	Cyperaceae	0.47	51.00	9.00	50.00	0.29	0.55	8.42
Plantago nivea	Plantaginaceae	0.00	35.00	25.00	34.00	0.51	0.22	2.14
Aristida adscensionis	Poaceae	0.62	6.00	14.00	28.00	0.01	0.01	0.00
Muhlenbergia peruviana	Poaceae	0.40	1.00	1.00	1.00	0.05	0.01	0.00
Bouteloua chondrosioides	Poaceae	0.34	0.00	0.00	1.00	0.00	0.00	1.75
Bouteloua polymorpha	Poaceae	0.48	4.00	1.00	4.00	0.00	0.00	3.67
Microchloa kunthii	Poaceae	0.72	5.00	16.00	30.00	0.00	0.00	4.66
Sporobolus tenuissimus	Poaceae	0.00	1.00	0.00	19.00	0.34	0.58	6.30
Crusea diversifolia	Rubiaceae	0.00	23.00	16.00	24.00	0.26	0.08	0.00
Richardia tricocca	Rubiaceae	0.00	0.00	2.00	16.00	0.34	0.23	6.45

Table 2. ΔWAIC values for the models that describe the effects of the different measured traits on the ability of species to buffer competition ($\log(b_j)$). Models with ΔWAIC = 0 were the models with the best support to the data.

Explanatory variable	no random effect	Intercept	Intercept and slope
Intercept (null model)	19.2	10.4	-
Standarized seed bank size	20.4	12.2	12
Mean life expectancy	19.3	12.8	0
Seed soil survival at 18 months	17.8	11.6	5.3
Seed soil survival at 30 months	21.5	10.1	7.6

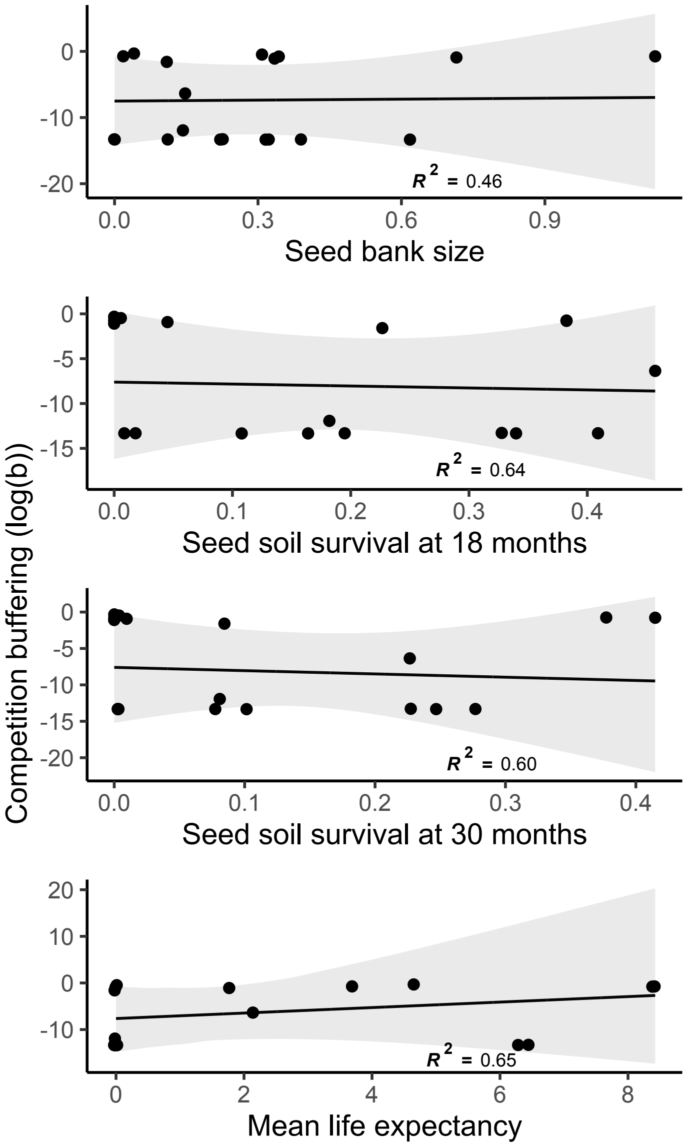

Figure 1. Relationship between the size of the seed bank, the survival of the seeds in the soil, mean life expectancy and the potential of species to buffer competition. Envelopes corresponded to 95% credibility intervals.

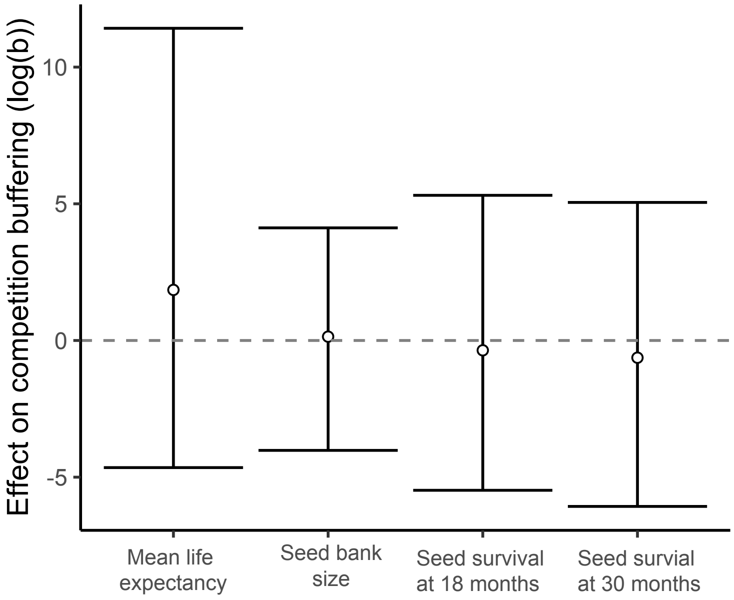

Figure 2. Mean of each of the explanatory variables and their 95% credibility intervals.

Appendix 1. Bayesian *R* squared posterior.

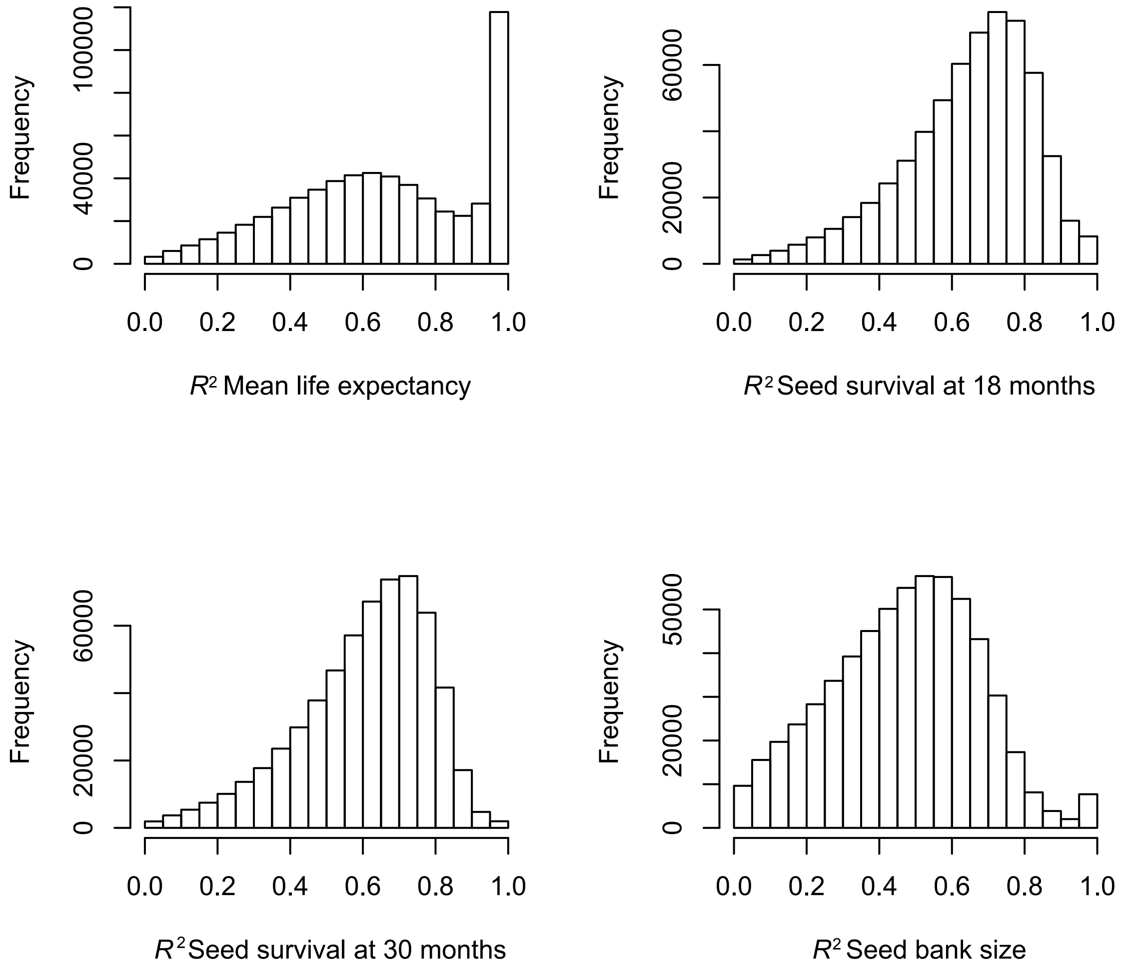

Fig. S1.1 The posterior distribution of Bayesian R^2 for each explanatory variable.

Discusión General

En este estudio se buscó evaluar el efecto de las fluctuaciones interanuales, las relaciones filogenéticas y algunos atributos de historias de vida sobre la coexistencia estable de 19 especies de un pastizal semiárido. Se encontró que la variabilidad ambiental no juega un papel preponderante en su coexistencia. Son las diferencias en la intensidad de la competencia intra e interespecífica lo que determina el mantenimiento de la diversidad en este pastizal semiárido, seguido de la no linealidad relativa (Zepeda y Martorell 2019). Las relaciones filogenéticas entre las especies sí parecen ser relevantes para su coexistencia, pero sólo en comunidades altamente diversas (Zepeda y Martorell 2021). Por último, la longevidad de los individuos disminuye los efectos negativos conjuntos de la competencia y las condiciones ambientales desfavorables (Zepeda *et al*. en preparación). En contraste, los bancos de semillas no parecen jugar un papel preponderante para el amortiguamiento de la competencia e incluso la evidencia sugiere que podrían impedirlo.

El efecto de almacenamiento no promueve la coexistencia de especies en el pastizal

Los resultados obtenidos en este estudio descartan la hipótesis de que el efecto de almacenamiento sea el principal responsable del mantenimiento de la diversidad en el sistema de estudio. Los tres capítulos de la tesis aportan evidencia de que esto se debe a que las condiciones necesarias para que este mecanismo promueva la coexistencia de especies —diferentes respuestas al ambiente, covarianza clima-competencia y amortiguamiento de la competencia— no se cumplen.

En el capítulo I se determinó que el efecto de almacenamiento fue el mecanismo de menor importancia para el mantenimiento de la diversidad vegetal. En el capítulo II y III, se observó que sólo los pastos y las ciperáceas pueden amortiguar los efectos de la competencia. Mientras que el 58% restante, presentaron valores de subaditividad (valores del parámetro *b*) iguales a cero. En consecuencia, el efecto de almacenamiento no puede estabilizar su coexistencia. En el capítulo I y II, también se encontró que las tasas de crecimiento poblacional de la mayoría de las especies están correlacionadas en el tiempo, lo que implica que los años buenos para una especie también son buenos para sus vecinos. Esto repercute en la intensidad de la competencia que experimenta una especie. Al haber más individuos interactuando, la competencia por los recursos será aún más fuerte. Estudios teóricos han demostrado que cuando hay alta sincronicidad entre las especies, éstas no pueden aumentar sus tamaños poblacionales cuando se encuentran a bajas densidades debido a que la competencia inhibe su crecimiento. Por consiguiente, las especies presentan covarianzas clima-competencia positivas, contrario a lo requerido por el efecto de almacenamiento. Este efecto podría ser más severo si los individuos con los que hay interacción son parientes cercanos, ya que la competencia sería más intensa.

La variabilidad interanual no parece ser muy relevante para el mantenimiento de la diversidad en el sitio de estudio. Sólo tres especies presentaron contribuciones importantes del efecto de almacenamiento, y en los tres casos estas contribuciones fueron negativas. Las contribuciones de los mecanismos de coexistencia dependientes de las fluctuaciones (efecto de almacenamiento y no linealidad relativa) fueron en general poco relevantes para la coexistencia. Quizás esto se deba a la elección de las especies de estudio. Las 19 especies de estudio son las 19 especies más abundantes en el pastizal. Se trabajó con esas especies debido a que eran las que tenían más datos, lo que facilita y provee mayor robustez a la parametrización de los modelos de dinámica poblacional. No obstante, los estudios teóricos han demostrado que el efecto de almacenamiento podría ser muy relevante para la estabilización de la coexistencia de especies "raras" o que se encuentran poco representadas en las comunidades (Kelly y Bowler 2002). Esto se debe a que son más sensibles a la variabilidad temporal y, en consecuencia, pueden aprovechar las ventanas de oportunidades para aumentar sus tamaños poblacionales. También, cabe destacar que el modelo utilizado en el presente estudio no contempla los efectos de la autocorrelación interanual. Esto podría resultar en una subestimación de los mecanismos dependientes de las fluctuaciones, ya que la dinámica poblacional a largo plazo y sus efectos en la comunidad podrían no ser los mismos si las especies experimentan consecutivamente varios años de condiciones benignas o desfavorables. Por ejemplo, se ha reportado que en los pastizales de California, la persistencia de las herbáceas en la comunidad se ve severamente amenazada cuando experimentan condiciones ambientales benignas de manera continua (Levine y Rees 2004). Esto debido a que la competencia con los pastos se vuelve más intensa, disminuyendo las probabilidades de que las especies de herbáceas aprovechen las condiciones favorables del ambiente para aumentar sus tamaños poblaciones.

El presente estudio destaca por evaluar rigurosamente las tres condiciones del efecto de almacenamiento. En la mayoría de los trabajos en los que se ha evaluado experimentalmente y con datos de campo el concepto de efecto de almacenamiento se han enfocado en determinar si hay respuestas especie-específicas al ambiente, si hay presencia de fluctuaciones en la abundancia relativa de los individuos (Descamps-Julien y González 2005; Secor 2006), fluctuaciones en las tasas intrínsecas de crecimiento (Adler *et al.* 2006; Adler *et al.* 2009), fluctuaciones en el éxito reproductivo (Pake y Venable 1995, 1996; Angert *et al.* 2009) o fluctuaciones en las tasas de germinación (Pake y Venable 1995, 1996; Adondakis y Venable 2004). La mayoría de los estudios se han realizado en comunidades vegetales (Pake y Venable 1995, 1996; Adondakis y Venable 2004; Levine y Rees 2004; Facelli *et al.* 2005; Adler *et al.*

2006; Adler *et al.* 2009; Angert *et al.* 2009; Armitage y Jones 2019), y algunos han estudiado detalladamente las restricciones germinativas y dinámicas de los bancos de semillas (Bonis *et al.* 1995; Pake y Venable 1995, 1996; Levine y Rees 2004; Facelli *et al.* 2005). Sin embargo, determinar si hay o no hay diferenciación temporal de nicho no es suficiente para determinar que el efecto de almacenamiento promueva la coexistencia de especies. También es necesario evaluar si dicha diferenciación contribuye al amortiguamiento de la competencia entre individuos con- o heteroespecíficos cuando las condiciones ambientales no son favorables, que es el elemento clave en el efecto de almacenamiento. Analizar las fluctuaciones en las tasas vitales a lo largo del tiempo sólo refleja los efectos de las fluctuaciones temporales sobre la dinámica de una población, pero no evalúa directamente las interacciones entre especies (Chesson y Huntly 1989; Chesson 2003) ni es, por sí sólo, evidencia de efecto de almacenamiento. En todos los casos, la condición de amortiguamiento de la competencia se ha evaluado de modo indirecto y cualitativo.

La filogenia de las especies afecta la estabilidad de la coexistencia

Los resultados obtenidos en el capítulo II apoyan la hipótesis de que la filogenia de las especies influye en la intensidad de los mecanismos de coexistencia. Sin embargo, el poder explicativo de la cercanía evolutiva entre las especies fue débil debido a la gran variación en los comportamientos de las especies de estudio. La intensidad y el efecto (positivo o negativo) de la distancia filogenética sobre las contribuciones de los mecanismos de coexistencia y la tasa de crecimiento poblacional a largo plazo fue muy variable entre especies. Para algunas de ellas, la estabilidad de la coexistencia, así como la intensidad de los mecanismos que la subyacen aumentaban conforme disminuía su grado de parentesco. Mientras que para otras especies ocurría lo contrario. La estabilidad de la coexistencia se favorecía entre especies cercanamente emparentadas.

La poca influencia del efecto de la distancia filogenética sobre el mantenimiento de la diversidad vegetal refleja los patrones de los ingredientes que la subyacen. Si bien se encontró evidencia de señal filogenética en las respuestas demográficas de las especies, la intensidad de la competencia, las covarianzas clima-competencia y el amortiguamiento de la competencia; cabe señalar que los efectos tampoco fueron muy marcados en todos los casos. Esto podría deberse, al menos en parte, a lo siguiente: 1) El gradiente filogenético necesita estar mejor representado. 2) las especies lejanamente emparentadas tienen características similares que resultan en desempeños similares, es decir, hay convergencia (Donoghue 2008; Cavender-Bares *et al.* 2009). 3) Las interacciones locales no están fuertemente reguladas por la estructura filogenética (Prinzing *et al.* 2008). 4) La competencia no resulta en exclusión competitiva o en una fuerte disminución en el desempeño de las otras especies sino en el desplazamiento de caracteres (Silvertown *et al.* 2006).

A pesar de que la evidencia respecto al efecto de la distancia filogenética sobre la coexistencia de especies podría considerarse poco clara, la relevancia de este estudio radica en la contribución de un marco teórico nuevo sobre cómo la filogenia podría afectar los distintos mecanismos de coexistencia descritos en la teoría moderna de la coexistencia. Además, lo que sí es claro es que el número de especies que se encuentran interactuando en la comunidad afecta las contribuciones de los mecanismos de coexistencia y, en consecuencia, su estabilidad. Tema que se ha debatido ampliamente en la ecología de comunidades y en el que la evidencia en comunidades altamente diversas aún es escasa.

En este capítulo también se demostró que la sincronía de las especies puede tener efectos opuestos sobre su persistencia en la comunidad. Por un lado, la sincronización desestabiliza a la coexistencia a través del efecto de almacenamiento. Mientras que, para otras especies, la sincronización en sus respuestas al ambiente promueve la coexistencia estable por medio de la no linealidad relativa, probablemente como resultado del incremento en las fluctuaciones en la competencia. Estos resultados, en conjunto con la evidencia de que las especies cercanamente emparentadas se sincronizan más, sugieren que el efecto de almacenamiento podría obstaculizar la coexistencia de especies cercanamente emparentadas, favoreciendo la diversidad filogenética en las comunidades. Por el contrario, la no linealidad relativa podría ser relevante para la coexistencia de especies cercanamente emparentadas y reducir la diversidad filogenética .

La longevidad de los individuos contribuye al amortiguamiento de la competencia, pero no los bancos de semillas

Durante mucho tiempo, se ha pensado que la presencia de ciertas etapas persistentes del ciclo de vida de las especies amortigua los efectos de las variaciones temporales. Esto favorece la coexistencia de especies por medio del efecto de almacenamiento. Sin embargo, la evidencia en contra o a favor es prácticamente nula. Debido a este hueco en la literatura, en el capítulo tres se evaluó la relación entre la esperanza de vida promedio, la supervivencia de los bancos de semillas en el suelo y la capacidad de las especies para amortiguar los efectos negativos de la competencia en años desfavorables.

Como se esperaba, se encontró que especies con esperanzas de vida promedio más altas tienen mayor potencial de amortiguamiento (valores muy positivos del parámetro *b*). Por el contrario, las especies con semillas que tienen mayor probabilidad de sobrevivir tienen menor potencial de amortiguamiento, aunque la tendencia fue débil. Mientras que el tamaño de los bancos de semilla no mostró ninguna relación. Estos resultados muestran que no hay que dar por sentado que la presencia de etapas de vida persistentes contribuye al amortiguamiento de la competencia en épocas desfavorables. Es necesario ser más rigurosos para probar esta condición de almacenamiento y determinar en qué condiciones sí puede haber amortiguamiento o no.

Seguir la dinámica de las semillas a largo plazo podría ser relevante para determinar su importancia en la persistencia de las poblaciones ya que se ha reportado que el comportamiento demográfico de los bancos de semillas puede variar ampliamente, y por lo tanto también su papel en el crecimiento poblacional y persistencia a largo plazo (Thompson y Grime 1979). Sin embargo, pocos estudios han cuantificado el impacto que pueden llegar a tener sobre las tasas de crecimiento poblacional. Probablemente esto se deba a la dificultad de medir las tasas vitales de los bancos de semillas (supervivencia y germinación). Por ejemplo, los experimentos que consisten en enterrar las semillas y exhumarlas después de cierto tiempo pueden sobreestimar las probabilidades de supervivencia de las semillas debido a que estas no estuvieron expuestas a todos los depredadores (Gross 1990; Thompson *et al.* 1997). En este estudio, se intentó reducir este efecto con un experimento de supervivencia de semillas en la superficie del suelo. Además de que en la naturaleza no todas las semillas se entierran e incluso no todas lo hacen con la misma probabilidad. Sin embargo, no fue posible monitorear el experimento por más de un año. Aún hace falta determinar un método más efectivo y generalizable para el estudio de los bancos de semillas.

Otro elemento importante en el estudio de los bancos de semillas y su papel en las tasas de crecimiento poblacional a largo plazo es la pérdida de la habilidad competitiva. Hasta el momento, los efectos negativos del envejecimiento de las semillas no se han incorporado explícitamente en los modelos demográficos ni en los modelos de historia de vida de las especies con bancos de semillas (Rice y Dyer 2001). En general, ningún modelo supone que haya diferencias en el vigor o en la habilidad competitiva entre semillas de diferentes edades. Sin embargo, esto podría resultar de vital importancia. Por ejemplo, se ha reportado que, en ambientes competitivos, los retrasos en la emergencia pueden tener fuertes efectos en el desarrollo individual y las jerarquías competitivas (Ross y Harper 1972).

Conclusiones

Este trabajo resalta la importancia de determinar la contribución relativa de diferentes mecanismos a la coexistencia y aporta evidencias de que varios mecanismos actúan simultáneamente y no siempre en el mismo sentido ni con la misma relevancia. También se enfatiza la importancia de estudiar la coexistencia de especies en sistemas con más de dos especies interactuando, ya que las conclusiones obtenidas en sistemas con poca diversidad no parecen sostenerse en sistemas altamente diversos.

A pesar de que la variabilidad temporal parece no ser crucial para la coexistencia de las especies de estudio, es importante resaltar los siguientes resultados: 1) El mecanismo dependiente de las fluctuaciones más importante para el mantenimiento de la diversidad fue la no linealidad relativa. 2) La sincronicidad entre las especies desestabiliza la coexistencia a través del efecto de almacenamiento, pero parece estabilizarla a través de la no linealidad relativa. 3) La no linealidad relativa podría ser relevante para el mantenimiento de la diversidad en comunidades con especies cercanamente emparentadas.

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