

TESIS DOCTORAL

*Reglas ecológicas de ensamblaje
en comunidades de plantas de
alta montaña*

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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: “**Reglas ecológicas de ensamblaje en comunidades de plantas de alta montaña**”, han sido realizados bajo su supervisión y son aptos para ser presentados por el licenciado Jesús López-Angulo ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en el Programa de Doctorado de Ciencias por la Universidad Rey Juan Carlos.

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A mi abuela

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Resumen



Antecedentes

Uno de los mayores desafíos que se vienen planteando los científicos desde el inicio de la Ecología es identificar los mecanismos responsables del ensamblaje de comunidades de plantas y esclarecer los determinantes que conducen la coexistencia local de las especies. Pese al esfuerzo realizado en construir un marco unificador que establezca cómo se ensambla la diversidad de plantas en las comunidades, el éxito ha sido relativamente escaso, y gran parte de culpa lo tienen ciertas limitaciones tanto descriptivas como analíticas.

El hecho de que los patrones de diversidad y sus determinantes varíen a diferentes escalas espaciales dificulta en muchas ocasiones el alcance de respuestas generales y hace que se obtengan resultados discrepantes cuando se intentan responder las mismas preguntas. Por tanto, para atajar eficazmente las preguntas relacionadas con el ensamble de comunidades de plantas es necesario aplicar un enfoque metodológico que permita el estudio simultáneo de un conjunto de escalas espaciales. A la problemática de las escalas, se suma la limitación de la que adolece una de las aproximaciones más usadas en ecología, la perspectiva taxonómica, que tiene que ver con la asunción subyacente de que todas las especies son funcionalmente equivalentes y evolutivamente independientes. De este modo, resulta ineludible la evaluación de las diferencias ecológicas y evolutivas que hay entre las especies de la comunidad para facilitar la manifestación de procesos ecológicos y evolutivos que determinan la composición de las especies en la comunidad.

Algunas limitaciones analíticas están asociadas con el uso de modelos nulos que tienen capacidad reducida para detectar procesos ecológicos específicos. Así surge la necesidad de avanzar hacia el desarrollo de algoritmos que tengan en cuenta las probabilidades de incidencia de las especies bajo una determinada fuerza ecológica para detectar la prevalencia de otros mecanismos no considerados por el algoritmo. Otra restricción en el avance en este campo tiene que ver con el hecho de que las respuestas de las comunidades de plantas a factores locales y los procesos subyacentes son muy idiosincráticos y varían a lo largo de los distintos sistemas montañosos debido a características regionales como el clima o la historia evolutiva de las especies de la comunidad. Por tanto, para comprobar si las respuestas de la comunidad al ambiente son generales o inherentes a las condiciones climáticas y la historia evolutiva, y así avanzar hacia un marco global, se deberían plantear las mismas preguntas en contextos regionales, pero con climas contrastados, y por otro lado en regiones con historias biogeográficas distintas pero con climas similares.

Objetivos

Nuestro objetivo es intentar arrojar luz en la búsqueda de las reglas ecológicas de ensamblaje en comunidades de plantas de alta montaña y la identificación de los principales mecanismos responsables que estructuran la diversidad, prestando especial atención a algunas de las limitaciones que restringen el progreso hacia un margo global para la teoría de coexistencia como son el problema de la escala espacial, la elección de modelos nulos adecuados y eficaces, y la replicación del estudio en regiones con distintas condiciones climáticas e historias biogeográficas.

Metodología

El estudio se centró en las comunidades plantas de alta montaña de cuatro cadenas montañosas, las cuales presentan diferente clima y/o historia evolutiva y biogeográfica. En España se muestrearon (1) 39 sitios en el Parque Nacional de la Sierra de Guadarrama influenciado por el clima Mediterráneo y (2) 27 sitios en el Parque Nacional de Ordesa-Monte Perdido con clima templado. Otras dos regiones fueron muestreadas en la cordillera andina en las que se muestrearon (3) 20 sitios en los alrededores del Valle Nevado y la Laguna del Maule en los Andes centrales de Chile e influenciado también por un clima Mediterráneo y (4) 17 sitios en el Parque Nacional Torres del Paine en el sur de la Patagonia caracterizado tipo por un clima Sub-antártico. En cada cadena montañosa se muestreamos a 3 escalas distintas las comunidades de plantas que se encuentran por encima del límite arbóreo cubriendo el gradiente altitudinal completo donde se produce este de ecosistema.

En cada unidad muestral se estimó la cobertura de cada especie. Cada sitio fue caracterizado por su altitud, la insolación incidente, la fertilidad del suelo y la prevalencia de las interacciones entre especies. Con todas las especies presentes en todas las cordilleras construimos un árbol filogenético utilizando dos loci (*rbcL* y *matK*) para caracterizar la estructura filogenética de las comunidades. Por otro lado, se midieron 7 rasgos funcionales que esperamos que respondan a las condiciones ambientales, para las especies más abundantes en cada cordillera: (i) la altura vegetativa máxima (*Hmax*), (ii) el tamaño de la planta (*IS*), (iii) el área foliar específica (*SLA*), (iv) el contenido de materia seca foliar (*LDMC*), (v) el grosor de la hoja (*LT*), (vi) el área de la hoja (*LA*) y el peso de la semilla (*SM*). Con la información de abundancias, el árbol filogenético y los rasgos, se calcularon índices de diversidad taxonómica, funcional y filogenética. La respuesta de estas métricas a los factores ambientales fue estudiada principalmente usando modelos lineales y modelos de ecuaciones estructurales.

Resultados

La riqueza de especies respondió de manera unimodal a la altitud a lo largo de distintas latitudes de los Andes Chilenos cuando fue evaluada a escalas grandes. Otros factores como las interacciones bióticas influyeron solo a escalas pequeñas. La altitud y la insolación provocaron divergencia funcional y filogenética en los Andes Mediterráneos de Chile, sin embargo, la interacción de estos dos factores produjo una convergencia funcional y filogenética. A pesar del acople de los dos tipos de diversidades la señal filogenética fueron menor que las esperada bajo un modelo de movimiento browniano de la evolución del rasgo. Por otro lado, encontramos discrepancias entre la diversidad funcional observada y esperada para algunos rasgos funcionales cuando se generaron comunidades aleatorias con probabilidades de ocurrencias de las especies en función de sus óptimos ambientales en el PN de Ordesa y Monte Perdido. Además, estas discrepancias se estructuraron a lo largo de distintos gradientes ambientales. Por último, cuando se compararon las relaciones entre los tres componentes de la diversidad (taxonómica, funcional y filogenética) y los factores abióticos y biótico, en zonas que difieren en clima e historia biogeográfica, se encontraron algunas relaciones más o menos constantes, pero la idiosincrasia fue el patrón predominante.

Conclusiones

La estructura de las comunidades de plantas alpinas subyace a las reglas ecológicas de ensamblaje, tanto bióticas y como abióticas. De este modo, los principales mecanismos que determinan la estructura de las comunidades de plantas de alta montaña en nuestras zonas de estudios son un complejo equilibrio entre competencia y facilitación que se produce en respuesta a la variabilidad en las condiciones ambientales, junto con el filtrado ambiental que producen las bajas temperaturas de alta montaña. En ocasiones, a pesar de encontrar los mismos patrones de ensamblaje en regiones con distinto clima, los mecanismos responsables pueden diferir. En otras ocasiones las relaciones entre la comunidad y sus determinantes pueden ser totalmente idiosincráticos llegando a encontrar relaciones completamente opuestas. El efecto de los determinantes bióticos y abióticos en la diversidad taxonómica ve incrementada su intensidad a escalas espaciales específicas debido a que los procesos subyacentes al ensamblaje actúan a diferentes escalas espaciales. Por ejemplo, la altitud influye a la diversidad taxonómica a mayor escala que las interacciones bióticas, cuyo efecto se detecta a las escalas finas donde las interacciones entre plantas se dan.

Nuestros resultados sugieren que al menos en resoluciones espaciales pequeñas, las interacciones bióticas son un factor crítico del ensamblaje de las comunidades del centro de

Pirineos, que dejan una huella detectable en la estructura funcional de rasgos como la altura máxima de la planta o el peso de las semillas. Así, el uso de modelos nulos que representan la acción de reglas abióticas simulando comunidades a partir de constricciones ambientales abióticas presentan un gran potencial para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia. Por otro lado, la evaluación de la dispersión funcional a lo largo de múltiples gradientes de estrés ayuda a interpretar los patrones encontrados, dado que diferentes mecanismos pueden producir los mismos patrones (p.e. la facilitación y la competencia pueden generar divergencia funcional). Además, considerar interacciones entre gradientes, ya sean aditivas o sinérgicas, pueden revelar nuevas perspectivas para los procesos de ensamblaje de las comunidades. Por ejemplo, la interacción entre la altitud y la insolación produce divergencia funcional y filogenética como resultado de las interacciones facilitadoras donde las condiciones son más estresantes. Por el contrario, cuando las condiciones son más suaves, el dominio de unas pocas especies que son más competitivas podría conducir a patrones de convergencia funcional.

Introducción general



Uno de los mayores desafíos que se vienen planteando los científicos desde Darwin and Wallace es dilucidar cuáles son los procesos que originan y mantienen la diversidad biológica a todas las escalas espacio-temporales a lo largo de todo el planeta (Jaccard 1912; Connell 1978; Weiher & Keddy 1995; Ricklefs 2008). Las preguntas puestas sobre la mesa en las últimas décadas cubren un amplio abanico que va desde aquellas que tratan de esclarecer los procesos que determinan la variación de la biodiversidad a escalas regionales, pasando por aquellas que se focalizan en la organización de las comunidades, hasta aquellas que se centran en desentrañar los mecanismos y las reglas de ensamblaje que conducen la coexistencia local de las especies a las escalas más pequeñas (Keddy 1992; Weiher et al. 1998; Cavieres et al. 2006; Grace et al. 2011; Götzenberger et al. 2012; Fine 2015). Ya a principios del siglo pasado algunos de los primeros ecólogos en preocuparse por estas cuestiones sugerían que las comunidades ecológicas no se ensamblan al azar, y ponían en valor la existencia de procesos deterministas (Clements 1916; Phillips 1931). Por el contrario, otras corrientes de pensamiento contrapuestas y coetáneas de las anteriores consideraban que las comunidades son simplemente conjuntos de especies fruto de procesos estocásticos (Gleason 1939).

A pesar de que durante las últimas décadas se han desarrollado múltiples teorías para explicar la estructuración de las comunidades desarrollando los marcos deterministas y estocásticos (Shipley & Keddy 1987; Hubbell 2001; Lortie et al. 2004), el debate sigue siendo tan polémico como lo fue hace casi un siglo. Si bien, en la actualidad la controversia se centra en dos diferentes enfoques teóricos (Tilman 2004; Leibold & Mcpeek 2006; Chase 2014; Li et al. 2015), la teoría de nicho ecológico y la teoría neutral de la biodiversidad. El primero, de mayor tradición y peso histórico, se basa principalmente en las respuestas de las especies que forman la comunidad al ambiente tanto abiótico como biótico. De este modo, la diferenciación de nicho entre las especies explicaría la biodiversidad a diferentes escalas involucrando una gran cantidad de factores como los recursos edáficos, el clima y los competidores (MacArthur & Levins 1967; Chase & Leibold 2003). Por otro lado, la teoría neutral de la biodiversidad sugiere que todas las especies son idénticas en su eficacia biológica o “*fitness*” de especie y en el efecto que tienen unas sobre otras (Hubbell 2001) y se basa en la capacidad de los organismos para dispersarse y alcanzar un lugar por puro azar. Bajo esta perspectiva, los eventos evolutivos y biogeográficos junto con los estocásticos tienen un papel central en la estructuración de las comunidades.

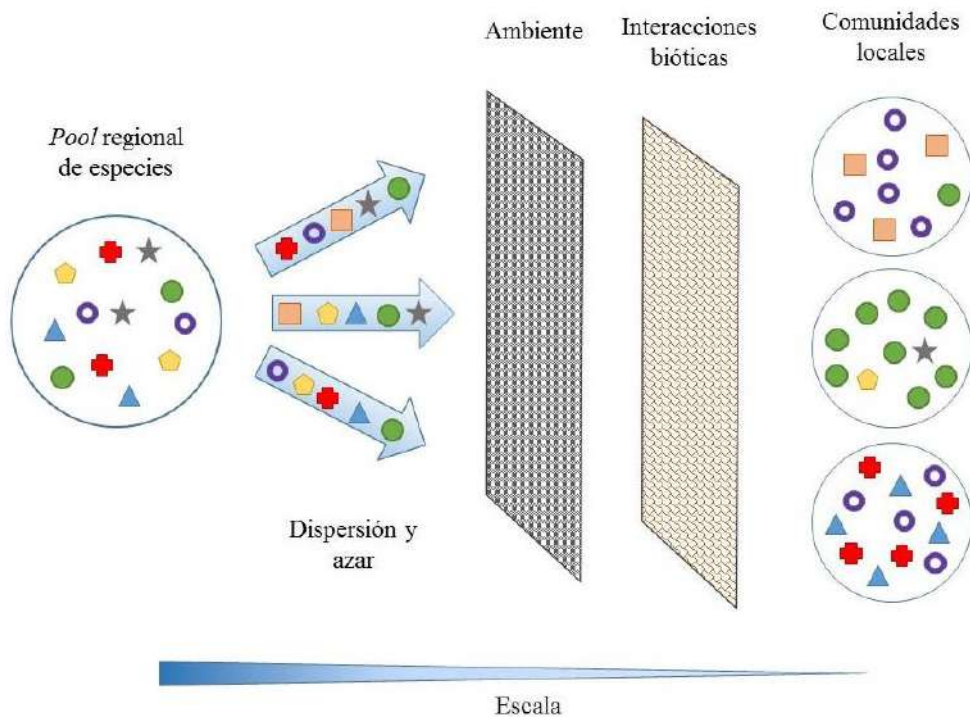
Recientemente, hemos comprendido que la organización de la diversidad es respuesta simultánea a procesos de los dos tipos (Escudero & Valladares 2016) y que la existencia de estas discrepancias teóricas como ya indicó Chase (2014) podrían ser en realidad una respuesta a los

diferentes tamaños de las ventanas espaciales a las que la biodiversidad es evaluada. Así, tenemos más claro que la escala de observación altera nuestra percepción de la importancia relativa de los procesos neutrales y de nicho. Por tanto, puesto que los patrones de diversidad y sus determinantes varían a diferentes escalas espaciales (Ricklefs 1987; Holt 1993; McGill 2010a; Harmon & Harrison 2015), la respuesta a las preguntas relacionadas con el ensamblaje de comunidades, desde las realizadas por biogeógrafos hasta las de los ecólogos de comunidades interesadas en lo que ocurre individuo a individuo, implica la integración y la necesidad de aplicar un enfoque metodológico que permita el estudio simultáneo de un conjunto de escalas espaciales, desde distribuciones regionales resultado de complejos procesos históricos y evolutivos, hasta las escalas más pequeñas en las que las interacciones planta a planta son críticas.

Llegados a este punto, y como se menciona arriba, el paradigma actual sugiere que el ensamblaje de las comunidades locales es el resultado de la existencia de un complejo equilibrio entre procesos deterministas y estocásticos que subyacen a ambas teorías (Chase et al. 2011; Vellend et al. 2014; Escudero & Valladares 2016) y cuya fuerza relativa e importancia varía a lo largo de las escalas espaciales y temporales (Ricklefs 1987; Levine 1992; McGill 2010a; Chase 2014). Por un lado, el marco teórico actual sugiere que los procesos ligados a las denominadas reglas filogeográficas, como los procesos biogeográficos y los eventos macro-evolutivos, son responsables de la configuración de los patrones de diversidad a grandes escalas, o lo que es lo mismo, son responsables de la formación del conjunto de especies, riqueza, o “*pool*” regional de especies que será el sustrato sobre los que operarán procesos que actuarán a escalas menores (Zobel 1997; Chesson 2000; Ricklefs 2004; Chase & Myers 2011). En consecuencia, a escalas pequeñas, son los procesos ecológicos que subyacen a las denominadas reglas ecológicas de ensamblaje (Diamond 1975; Keddy 1992) junto con procesos estocásticos como la extinción aleatoria y la deriva ecológica, los que determinan la estructura final de las comunidades locales (Tilman 2004; Chase 2014). La introducción de la noción de reglas ecológicas es una aportación muy sugerente de Diamond (1975) quien propuso tras observar patrones de coocurrencia en especies de aves, la existencia de mecanismos predecibles que organizan la coexistencia de las especies en las comunidades. Es un concepto simple y fácil de entender que ha sido dotado de contenido a lo largo de los últimos 40 años. Las reglas ecológicas se dividen en las reglas de dispersión, las reglas abióticas y las reglas bióticas (Götzenberger et al. 2012). Así, la actual metáfora equipara conceptualmente los procesos selectivos (no entenderlo como un proceso evolutivo) o reglas con “*filtros*” que actuarían de forma jerárquica y a escalas cada vez más finas para imponer la estructura de la diversidad en el ensamblaje de las comunidades (Wilson 1999;

Götzenberger et al. 2012; HilleRisLambers et al. 2012). De una manera muy esquemática, el conjunto de especies que pueden existir en un lugar concreto sería determinado a partir del *pool* regional en función de la limitación de la dispersión de las especies (*dispersal rules*). Posteriormente, las limitaciones que imponen el ambiente sobre las especies capaces de colonizar dicha localidad determinan la composición a escalas aún más pequeñas (*abiotic rules*). Y por último, a esas escalas donde las especies interactúan unas con otras se producen relaciones tanto positivas como negativas (*biotic rules*) que promueven o limitan la coexistencia de las especies (Fig. 1) (MacArthur & Levins 1967; Grime 1973).

Figura 1. Esquema de los procesos de ensamblaje que actúan a distintas escalas mediante los cuales se forman las comunidades locales a partir del pool regional de especies (modificado de HilleRisLambers et al. 2012).



No hay duda de que en las últimas décadas con la aparición de la ecología basada en rasgos y la integración de la información filogenética se han experimentado grandes progresos en la construcción de lo que se ha denominado la "Teoría de Coexistencia" (HilleRisLambers et al. 2012). De esta forma, para identificar los procesos que gobiernan las comunidades hemos pasado de tener en cuenta básicamente la acumulación de información taxonómica, es decir, cuantificar

el número de especies y las distribuciones de sus abundancias en el tiempo y en el espacio (p.e. Rosenzweig 1995; Willig et al. 2003), a considerar el papel de cada especie en la comunidad en función de sus rasgos funcionales y sus relaciones evolutivas, entendiendo que las reglas de ensamblaje van a operar fundamentalmente a través de dichos atributos (Keddy 1992; Webb et al. 2002). De esta manera, se supera la idea poco realista de que todas las especies son ecológicamente equivalentes y evolutivamente independientes (Pavoine et al. 2010; Swenson 2011). En este sentido, cabe destacar la explosión de trabajos publicados en las dos últimas décadas que han utilizado la aproximación funcional y/o filogenética con la intención de esclarecer las reglas que rigen el ensamblaje de las comunidades en un elenco completo de ecosistemas y regiones biogeográficas (Webb et al. 2002; Lepš et al. 2006; Swenson et al. 2006; Kraft et al. 2007; Pillar & Duarte 2010; Mason et al. 2012).

La ecología basada en rasgos funcionales se fundamenta en la idea de que las especies participan en la comunidad y responden a las presiones ecológicas selectivas en función de sus atributos funcionales (Cornwell & Ackerly 2009; Shipley et al. 2016). Estos atributos funcionales reflejan las estrategias ecológicas de las especies ya que están relacionadas con características morfológicas, fisiológicas y fenológicas de las especies que resultan claves para su desempeño en los hábitats que ocupan (Violle et al. 2007). Sin duda, estas características hacen de los rasgos funcionales una buena herramienta para responder preguntas relacionadas con la existencia y detección de las reglas de ensamblaje tanto bióticas como abióticas. Por ejemplo, la ecología funcional basada en rasgos permite detectar la existencia de una fuerza abiótica conocida como filtrado ambiental la cual impulsa la coexistencia de especies funcionalmente similares excluyendo las especies que no están dotadas de los rasgos necesarios para persistir en esas condiciones (Lavorel & Garnier 2002; Mayfield et al. 2009). Por otro lado, la competición tenderá a evitar la coexistencia de especies demasiado similares entre sí, desde un punto de vista funcional (MacArthur & Levins 1967; Chesson 2000). Una de las limitaciones que presenta la ecología funcional es que a menudo algunos rasgos que son importantes en el desempeño de la planta en la comunidad no son considerados por desconocimiento o por falta de recursos para medirlos o estimarlos. Por esta razón, la relación de parentesco entre especies se usa como una medida de similitud ecológica bajo la premisa de que las especies emparentadas estrechamente serán ecológica y funcionalmente más similares que los parientes más distantes (Webb et al. 2002; Losos 2008; Burns & Strauss 2011). Por tanto, aunque el uso de filogenias ha permitido inferir eventos históricos como la diversificación de especies (Davis et al. 2002; Hughes & Eastwood 2006), la cuantificación de la relación filogenética entre especies se ha usado en numerosas ocasiones para desentrañar los procesos ecológicos que gobiernan el ensamblaje de

comunidades a escalas espacio-temporales pequeñas (Hardy 2008; Mayfield & Levine 2010; Le Bagousse-Pinguet et al. 2017).

Una de las metodologías más usadas y potentes para detectar la existencia de reglas ecológicas de ensamblaje en conjunto con la aproximación funcional y filogenética (ambas se basan en las distancias de similitud entre especies) es el uso de modelos nulos (Gotelli & Graves 1996). Este enfoque se basa en la comparación de la distribución observada de los rasgos funcionales (de la relación filogenética o de cualquier característica de la comunidad observada) con distribuciones nulas generadas al imponer restricciones a la aleatorización para conservar solo ciertas características de los datos (Gotelli & Graves 1996; Ackerly & Cornwell 2007; Kraft et al. 2007; de Bello 2012). De esta manera, si las especies que forman la comunidad son más parecidas ecológicamente o están más emparentadas de lo que cabría esperar dado un modelo nulo, se pueden inferir procesos como el filtrado abiótico o la exclusión competitiva (Diaz et al. 1998). La existencia de divergencia funcional o filogenética podría estar revelando la importancia de la diferenciación de nicho en la determinación del ensamblaje, o incluso de facilitación entre las especies que componen la comunidad (Valiente-Banuet & Verdú 2007; Kraft et al. 2008). Este último ejemplo, pone de manifiesto el problema que tiene esta aproximación, ya que la interpretación de los patrones generados bajo un modelo nulo, en ocasiones se hace complicada ya que los mismos patrones pueden ser producidos por distintos mecanismos.

Pese a la potencia de los modelos nulos para dilucidar si los patrones observados son congruentes con lo que cabría esperar por azar, hay una gran cantidad de algoritmos y esquemas de aleatorización que dificultan su elección y la llegada de un consenso metodológico mediante el cual abordar las preguntas ecológicas que subyacen el ensamblaje de las comunidades (Ulrich & Gotelli 2013; Ulrich et al. 2017). Estos modelos varían desde aquellos que mantienen fija la frecuencia de ocurrencia de las especies hasta aquellos que fijan la riqueza de especies en las comunidades (Gotelli 2000; Gotelli & Entsminger 2003). Sin embargo, estos modelos nulos tienen una capacidad reducida para detectar procesos ecológicos específicos (Gotelli & Ulrich 2012) y en numerosas ocasiones identificar si los mecanismos que producen los patrones son bióticos o abióticos se hace complicado (Kraft et al. 2015; Cadotte & Tucker 2017). En los últimos años, aunque se ha logrado progresar significativamente en el desarrollo de nuevos algoritmos con un sentido ecológico más profundo y claro (Peres-Neto et al. 2001; Cornwell et al. 2006; de Bello et al. 2012; Chalmandrier et al. 2013; Miller et al. 2017), se mantiene la necesidad de avanzar hacia el desarrollo de algoritmos que reproduzcan los patrones que cabría esperar si operasen reglas de ensamblaje o mecanismos concretos. De este modo, si no ocurren

desviaciones de la configuración funcional (o filogenética) respecto a la configuración esperada bajo el modelo nulo con dichas características, quedaría reflejada la prevalencia del mecanismo (Gotelli & Ulrich 2012).

En este sentido, la alta montaña se presenta como un excelente sistema donde detectar las reglas ecológicas de ensamblaje ya que las comunidades de plantas alpinas que allí viven están sometidas a una predecible variación en las condiciones ambientales, que además ocurre en muy cortas distancias (Körner 2007; Sanders & Rahbek 2012). Así, pequeños cambios de altitud pueden significar grandes cambios en temperatura y humedad, pero también, variaciones en la distribución y duración del paquete de nieve o incluso de la longitud del período vegetativo en el cual las plantas pueden crecer y reproducirse (Körner 2003). Existen otros factores topográficos que son críticos en ambientes alpinos, como la pendiente o la orientación, que también pueden generar diferencias microclimáticas importantes (Copeland & Harrison 2015; Winkler et al. 2016). De hecho, uno de los patrones más ampliamente conocidos es el de la variación en la composición de especies que suele ocurrir en las distintas laderas de una montaña (Badano et al. 2005). Si bien, en la mayoría de los casos, el efecto que produce estos factores topográficos en la estructura de la vegetación tiene que ver con la incidencia de la radiación solar (Holland & Steyn 1975), en otros casos puede generar variación espacial en las propiedades del suelo (Yimer et al. 2006). Es precisamente la heterogeneidad ambiental relacionada con las propiedades del suelo otro importante estructurador de la diversidad de la vegetación que actúa a pequeñas escalas (Hutchings et al. 2009). En este sentido, especies en parches pobres de nutrientes en el suelo pueden ver limitado su desarrollo e incluso su supervivencia, mientras que en parches ricos se pueden desencadenar complejas interacciones de competencia (Theodose & Bowman 1997; Reynolds & Haubensak 2009). Sin ir más lejos, las interacciones bióticas juegan un papel clave en los procesos que gobiernan el ensamblaje de comunidades de plantas de alta montaña. Concretamente, la facilitación, cuya prevalencia tiende a aumentar con la severidad ambiental, y por tanto, con la altitud en los sistemas alpinos (Choler et al. 2001; Callaway et al. 2002; Schöb et al. 2013; Cavieres et al. 2014).

No podemos dejar de indicar que a pesar de la severidad de los ambientes alpinos, y del efecto general que producen los gradientes de estrés asociados a las montañas en las comunidades de plantas, sus respuestas locales y los procesos subyacentes varían a lo largo de los distintos sistemas montañosos debido a características idiosincráticas y factores de gran escala como el clima o la historia evolutiva de las especies de la comunidad (Wiens & Donoghue 2004; Safi et al. 2011). Por ejemplo, la sequía estival propia del clima Mediterráneo ejerce un papel de filtro ambiental muy intenso que puede condicionar la estructura y la composición de las

comunidades, sobre todo a cotas más bajas (Giménez-Benavides et al. 2007; Mihoč et al. 2016). Así, esta falta de agua en los momentos críticos para las plantas pueden limitar procesos como el establecimiento de las especies (Gutiérrez-Girón 2013) o las interacciones positivas (Schöb et al. 2013). Por otro lado, los mismos determinantes podrían producir distintos patrones de diversidad en diferentes regiones que comparten clima, debido a que actúan sobre grupos de especies (*pools* florísticos regionales) con distintas características de partida. Sin duda alguna, el alto grado de idiosincrasia ecológica asociada a las distintas regiones se presenta como una limitación de las que hasta ahora ha adolecido la búsqueda de reglas ecológicas de ensamblaje.

En definitiva, aunque se ha realizado un gran esfuerzo en avanzar hacia un marco global para el ensamblaje de las comunidades, el éxito ha sido relativamente escaso (McGill 2010b; Chacón-Labela et al. 2016) y son muchas las discrepancias que se encuentran en la literatura cuando se tratan de encontrar las reglas de ensamblaje en determinadas comunidades o entre algunas muy parecidas. Nosotros pensamos que una de las principales limitaciones en el avance en este campo tiene que ver con el hecho de que las escalas espaciales a las que se han abordado estas cuestiones son muy diferentes, y por tanto, los resultados que se han obtenido pueden ser discrepantes. A esto hay que sumarle que los clásicos modelos nulos que se han utilizado para atajar este tipo de preguntas no son capaces de reproducir patrones esperables tras la acción de determinados mecanismos o reglas, con lo cual separar los procesos que determinan los patrones encontrados puede ser una tarea imposible.

Conscientes de las limitaciones que restringen el progreso hacia una comprensión del ensamblaje de las comunidades, proponemos primeramente, evaluar el efecto de distintas variables abióticas y bióticas sobre la estructura de la comunidad a diferentes escalas espaciales, puesto que los procesos ecológicos como los estocásticos pueden variar entre escalas (Levine 1992; McGill 2010a). De este modo, esperamos encontrar el efecto de factores relacionados con el clima en la estructura de la comunidad cuando esta es evaluada a grandes escalas, mientras que a escalas más pequeñas el efecto de las interacciones bióticas debería tener mayor incidencia en las comunidades. Además, se hace necesaria la cuantificación del papel ecológico y del grado de parentesco filogenético de cada especie en la comunidad y así poder inferir las reglas de ensamblaje a partir de las estructuras funcional y filogenética que tienen las comunidades. Nuestras hipótesis nos hacen pensar que estas diversidades van a verse reducidas en los lugares más estresantes donde las condiciones son más duras (Díaz et al. 1998; Cavender-Bares et al. 2006; de Bello et al. 2009), mientras que en los lugares donde las condiciones son más suaves se esperaremos un incremento de la diversidad debida a la competencia (Webb et al. 2002; Kraft et al. 2008).

Parece primordial la necesidad de ir más allá de la generación de modelos nulos que suponen que los requisitos ambientales de las especies son similares (Gotelli & Ulrich 2012; Blois et al. 2014), y construir modelos nulos que consideren la estructura ambiental de los sitios ocupados (recuperación de las reglas abióticas de ensamblaje) y el tipo de interacciones que prevalece entre las distintas especies (reglas bióticas de ensamblaje). Así, esperamos encontrar discrepancias entre la diversidad funcional observada y la esperada por nuestros modelos nulos en aquellos sitios donde estos procesos de ensamble no sean capaz de explicar por si solos la configuración funcional. Además conscientes de la importancia que tienen el contexto climático y evolutivo en el que están embebidas las comunidades y los procesos que determinan su estructura, hemos seleccionado dos regiones con historias evolutivas y biogeográficas completamente diferentes (Europa / Sudamérica) y dentro de cada región dos cordilleras con climas contrastados para estudiar las relaciones entre la estructura de la comunidad y el ambiente. Específicamente, en cada región biogeográfica se ha seleccionado una cordillera de clima mediterráneo, el sistema central de la península ibérica y los Andes centrales, así como una sometida a clima templado, la montaña ártico-alpina de Pirineos y la subantártica de los Andes meridionales. Aquí esperamos encontrar relaciones generalizadas entre la altitud y los distintos componentes de la diversidad que estén relacionadas con la severidad térmica, mientras que otras relaciones únicas pueden darse entre la diversidad filogenética y los parámetros del suelo debido a su carácter idiosincrático. Pensamos que todo este planteamiento va a permitir desentrañar las reglas ecológicas de ensamblaje que organizan la coexistencia de las plantas en comunidades de alta montaña, o al menos, para ser más realistas, avanzar en este reto.

Objetivos

Nuestro objetivo es intentar arrojar luz en aquellos aspectos menos consolidados para una teoría global de coexistencia de especies de plantas, enfatizando la superación de las limitaciones expuestas anteriormente, e identificando reglas ecológicas de ensamblaje que subyacen a los patrones de diversidad de las comunidades. Nuestra idea motora es que las variaciones idiosincráticas en la detección de las reglas de ensamblaje en tipos concretos de comunidades pueden ser explicadas por cuestiones históricas y evolutivas. Para ello, nos basamos en el estudio de las comunidades de plantas de alta montaña, por ser un sistema muy rico en especies y cuyas peculiaridades ambientales hacen de él un modelo único para desentrañar los procesos deterministas que subyacen a las reglas ecológicas de ensamblaje y profundizar en la organización de estas reglas a través de las diferentes escalas espaciales. Concretamente el planteamiento adoptado en esta tesis nos permitirá conocer cómo el efecto de las variaciones

ambientales a pequeña escala interactúa con las condiciones climáticas y con la historia biogeográfica del territorio. En este sentido, las comunidades de alta montaña son muy parecidas estructuralmente, independientemente de la historia biogeográfica que ha determinado el pool florístico regional en cada una de ellas. Si además estudiamos dentro de cada región biogeográfica, montañas con climas muy contrastados (en nuestro caso climas mediterráneos frente a otros templados) podemos aislar algunos de los factores ambientales que pueden determinar los ensamblajes locales. Para enfrentarnos a este objetivo general hemos abordado los siguientes objetivos específicos:

- Analizar la variación de la diversidad taxonómica en comunidades de plantas de alta montaña (incluyendo la diversidad alfa y la beta) a lo largo de diferentes gradientes altitudinales situados en latitudes contrastadas de los Andes chilenos. Y determinar el grado en el que factores abióticos (la radiación solar y la heterogeneidad del suelo) y bióticos (interacciones entre especies) modulan los efectos de la latitud y la altitud identificando la escala espacial a la que se acentúan sus efectos. Los Andes chilenos representan un modelo ideal para estudiar la variación en estas comunidades dado que su disposición norte-sur ha permitido que las especies se desplacen durante los avatares climáticos homogenizando el pool florístico.
- Cuantificar la dispersión filogenética y funcional a lo largo de múltiples gradientes abióticos en las comunidades de plantas alpinas en los Andes Mediterráneos de Chile y evaluar la señal filogenética en los rasgos funcionales para esclarecer el grado en que la diversidad filogenética proporciona distinta información a la suministrada por la diversidad funcional. Las montañas Mediterráneas como las del centro de Chile presentan una fuerte sequía durante la época estival que se acentúa a bajas altitudes. Esta sequía se comporta como un filtro ambiental el cual podría afectar a la estructura funcional y filogenética.
- Detectar las reglas ecológicas de ensamblaje en las comunidades de plantas alpinas de los Pirineos Centrales generando modelos nulos que reproduzcan la estructura funcional que cabría esperar si operasen las reglas abióticas y bióticas. La vegetación de los Pirineos Centrales presenta una zonación de la vegetación muy marcada que sugiere la prevalencia de los procesos deterministas, y esto convierte a estas montañas en un buen modelo para encontrar las reglas ecológicas de ensamblaje.

- Explorar el efecto de los determinantes ambientales (elevación, nitrógeno total en el suelo, radiación solar y las interacciones bióticas) en la relación existente entre las diversidades taxonómica, funcional y filogenética mediante un modelo de ecuaciones estructurales, y comprobar si las relaciones en este complejo entramado son generales, o inherentes a las condiciones climáticas y la historia evolutiva por la cual se forman la riqueza de especies regional de las cuales se forman las comunidades locales.

Metodología general

Área de estudio

Para abordar los objetivos propuestos en la presente tesis doctoral, seleccionamos para su estudio las comunidades de plantas de alta montaña que ocurren en dos áreas de historia biológica diferente, la península ibérica y los Andes chilenos. En cada área se seleccionaron dos cordilleras de clima contrastado, la alta montaña mediterránea y la de clima templado (ártico-alpina y subantártica respectivamente). Este diseño permite contemplar la variación debida a diferencias macroclimáticas relevantes en comunidades que comparten *pool* florístico compartido en buena medida, y a su vez, permite analizar la importancia que tiene el origen histórico de *pool* florístico regional en comunidades influenciadas por regímenes climáticos parecidos.

De este modo, en la península ibérica se seleccionó el Parque Nacional de la Sierra de Guadarrama influenciado por el clima mediterráneo y (2) el Parque Nacional de Ordesa-Monte Perdido con clima templado. En la cordillera andina se muestrearon los alrededores del Valle Nevado y la Laguna del Maule en los Andes centrales de Chile, influenciados también por un clima mediterráneo y (4) el Parque Nacional Torres del Paine en el sur de la Patagonia caracterizado por un clima sub-antártico (Fig. 2). El clima mediterráneo de nuestras dos áreas se caracteriza por presentar una marcada estacionalidad y una intensa sequía estival que se hace más pronunciada a bajas altitudes, mientras que en las dos áreas templadas ocurren lluvias veraniegas con frecuencia.

En cada cadena montañosa se muestrearon las comunidades de plantas localizadas por encima del límite arbóreo, evitando pedregales y suelos rezumantes, cubriendo el gradiente altitudinal completo donde se produce este de ecosistema e intentando capturar la variabilidad local topográfica muestreando una amplia gama de orientaciones y pendientes. El límite altitudinal del dosel arbóreo depende de la latitud y la especie dominante entre otros factores. Así la altura a la que se encuentra este límite arbóreo varía desde los 500 m de altitud en el PN Torres del Paine, donde la especie dominante es el *Nothofagus pumilo*, a los 2200m al que se encuentra el límite de crecimiento de *Kageneckia angustifolia* en Farellones, hasta los ~1900 metros a los que se encuentran los bosques de *Pinus sylvestris* y de *Pinus uncinata* en los Parques Nacionales de la Sierra de Guadarrama, y Ordesa y Monte Perdido, respectivamente.

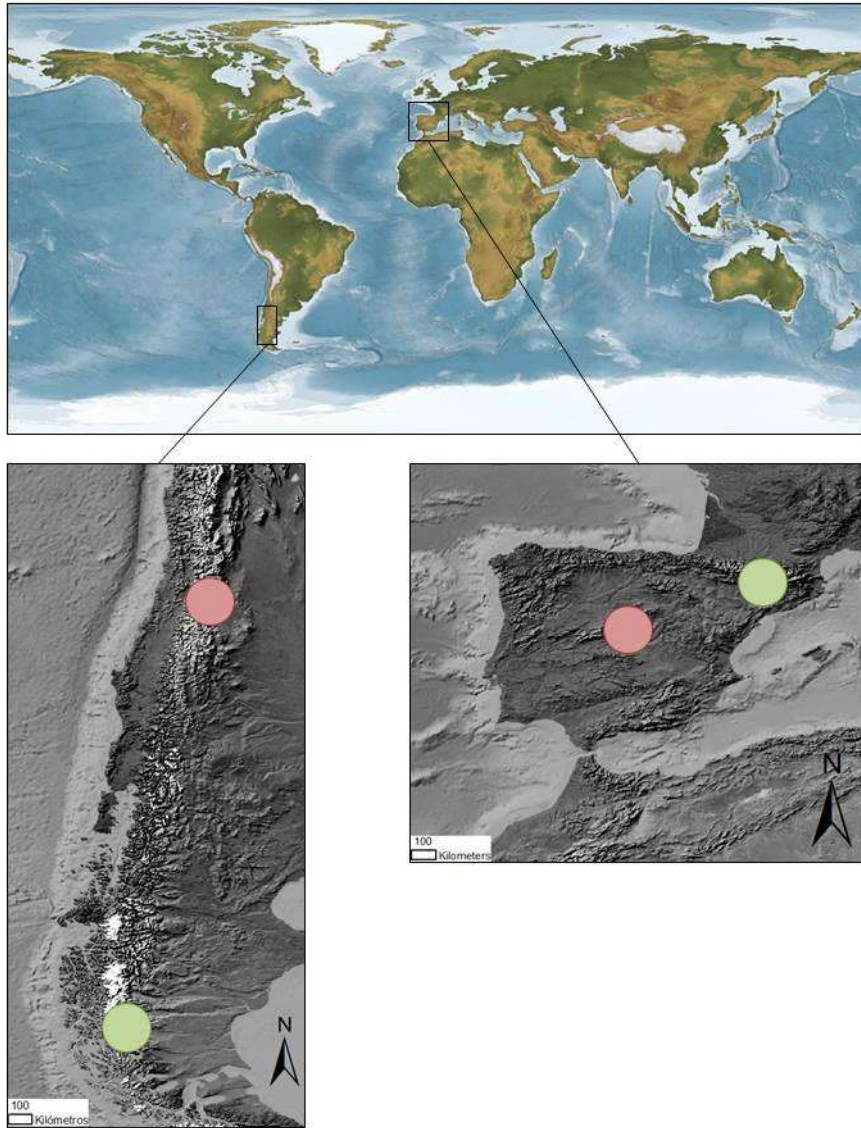


Figura 2. Ubicación de las cuatro localidades de estudio en los Andes chilenos y en la península ibérica. Los círculos rojos son las localidades influidas por el clima mediterráneo y los verdes por el clima templado.

La vegetación de las dos áreas geográficas (península ibérica y los Andes chilenos) difiere en composición debido a la diferente historia evolutiva mediante la cual se formaron los pools florísticos. Así, las dos áreas climáticas de cada región geográfica comparten un alto número de especies o al menos ocurren especies con alto grado de parentesco que divergieron tarde en la escala evolutiva. La vegetación de las dos áreas de estudio pertenecientes a la península ibérica está dominada por hierbas cespitosas del género *Festuca*. En el Sistema Central

predominan los pastos de *Festuca curvifolia* Lag. ex Lange la cual puede estar acompañada por un alto número de endemismos como *Jasione crispa* (Pourr.) Samp., *Pilosella vahllei* (Froel.) F.W. Schultz & Sch. Bip., *Minuartia recurva* (All.) Schinz & Thell., *Armeria caespitosa* (Gómez Ortega) Boiss. in DC (Fig 3).

Figura 3. Ejemplos de las comunidades dominadas por pastos de *Festuca curvifolia* en el Parque Nacional de la Sierra de Guadarrama en el Sistema Central



En Pirineos y especialmente sobre suelos calizos, predominan pastos de *Festuca gautieri* (Hackel) K. Richt. subsp. *scoparia* (Kerner ex Nyman) Kerguélen, acompañados de una amplia variedad de especies, entre las cuales destacan caméfitos rastreros y hemicriptófitos como *Sideritis hyssopifolia* L., *Androsace villosa* L., *Leontodon pyrenaicus* Gouan or *Thymus gr. serpyllum* L (Fig. 4).

Figura 4. Ejemplos de las comunidades dominadas por pastos de *Festuca gautieri* subsp. *scoparia* en el Parque Nacional Ordesa y Monte Perdido en los Pirineos.



Figura 5. Ejemplos de las comunidades dominadas por pastos de *Festuca acanthophylla* y *Azorella madreporica* en las inmediaciones de la laguna del Maule y en Farellones en los Andes chilenos, respectivamente.



A pesar de la diferente composición de las comunidades, las formas de vida vegetal e incluso los clados filogenéticos presentan un alto grado de similitud en las dos áreas geográficas. Así, en los Andes chilenos también abundan las especies de pastos de géneros como *Festuca* y *Poa* (Fig. 5). Sin embargo, la vegetación está dominada por cojines que pueden llegar a pasar los 5 metros, entre los que destacan varias especies de los géneros *Azorella* y *Bolax* (Fig. 5 y Fig 6), y arbustos postrados como aquellos de los géneros *Berberis* y *Empetrum* (Fig. 6), entre otras especies de los géneros *Nassauvia*, *Viola*, *Senecio*, *Acaena* o *Adesmia*.

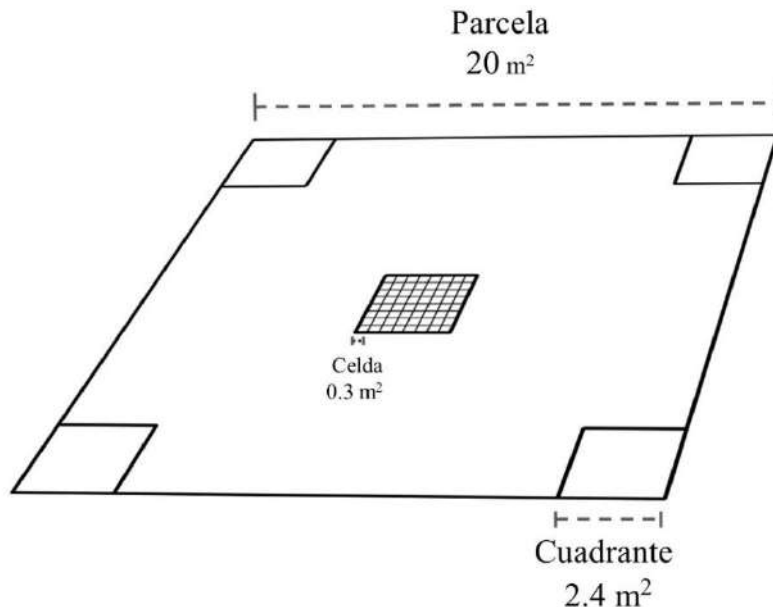
Figura 6. Ejemplos de las comunidades dominadas por *Empetrum rubrum* y *Azorella monantha* en el Parque Nacional de Torres del Paine, en los Andes patagónicos de Chile.



Muestreo de campo

En la península ibérica se muestrearon 39 sitios en el Parque Nacional de la Sierra de Guadarrama y 27 sitios en el Parque Nacional de Ordesa-Monte Perdido. En la cordillera andina se muestrearon 20 sitios los Andes centrales y 14 sitios en el Parque Nacional Torres del Paine. El estudio de vegetación se realizó a tres escalas diferentes: (1) escala de la parcela de 20 m x 20 m, (2) escala de cuadrante de 2.4 m x 2.4 m, y (3) escala de celda de 30 cm x cm. En cada uno de los 100 sitios se estableció una parcela y en cada parcela se establecieron cinco cuadrantes, colocados en las esquinas y un quinto en el centro. Este último cuadrante fue dividido en 64 celdas. En la figura 7 podemos ver un esquema del diseño de muestreo que se llevó a cabo en cada sitio.

Figura 7. Diseño de una parcela de muestreo y las tres escalas a las que se muestrearon la vegetación.



Para caracterizar cada sitio se midieron varias variables ambientales, de carácter tanto biótico como abiótico, que se usaron como predictores de la estructura de la comunidad. En particular, registramos la altitud como un subrogado de las condiciones climáticas, y calculamos un índice físico que estima la cantidad de insolación que recibe la ladera en función de la orientación y la inclinación (Gandullo 1974). Además, para evaluar edáficamente cada localidad y estimar la heterogeneidad espacial, se recogieron dos muestras de suelo (5 cm de diámetro por 10 cm de profundidad) en cada esquina de la parcela, una en zona desnuda y otra bajo vegetación. Después del secado y tamizado de las muestras, se evaluaron ocho propiedades del

suelo que están relacionadas con funciones ecosistémicas como la fertilidad del suelo, la productividad primaria y el reciclado de nutrientes (Maestre & Puche 2009; Delgado-Baquerizo et al. 2013). En particular, seleccionamos carbono orgánico (C), nitrógeno total (N), fósforo disponible (P), potasio (K), dos actividades enzimáticas (fosfatasa y la β -glucosidasa), el pH y la conductividad (Tabla 1).

Por último, el tipo de interacción entre especies fue considerado mediante la cuantificación del grado de segregación espacial en la coocurrencia de especies. Para ello calculamos el “*checkerboard score*” (C-score: Stone & Roberts 1990). Los valores altos de C-score indican que los pares de especies tienen a ocurrir de forma segregada, mientras que los valores bajos indican una tendencia de las especies a agregarse espacialmente.

Índices de diversidad

Construimos un árbol filogenético utilizando dos loci (rbcL y matK) para estimar las relaciones de parentesco entre las especies de nuestras comunidades y caracterizar su estructura filogenética. Por otro lado, se midieron 7 rasgos funcionales que responden a las condiciones ambientales en las especies más abundantes en cada cordillera: (i) la altura vegetativa máxima (Hmax), (ii) el tamaño de la planta (IS), (iii) el área foliar específica (SLA), (iv) el contenido de materia seca foliar (LDMC), (v) el grosor de la hoja (LT), (vi) el área de la hoja (LA) y el peso de la semilla (SM).

Con la información de abundancias, el árbol filogenético y los rasgos de las plantas se calcularon índices de diversidad taxonómica, funcional y filogenética. La diversidad taxonómica se cuantificó mediante la riqueza de especies, y el inverso del índice de concentración de Simpson (Dequiv). La riqueza de especies la cual tiene en cuenta el número de especies presentes en la muestra tiene la ventaja de ser muy fácilmente interpretable. Por otro lado, el Dequiv tiene en cuenta la abundancia de las especies por lo que la diversidad también tiene en cuenta la equitatividad. Para estimar la diversidad taxonómica y la funcional usamos la distancia media por pares o MPD y lo pesamos por la abundancia de cada especie.

Análisis estadísticos

Las técnicas estadísticas empleadas para analizar la relación directa entre los predictores ambientales y los distintos índices de diversidad han sido principalmente modelos lineales, desde los modelos lineales simples, los generalizados (GLMs), hasta los mixtos generalizados (GLMMs). explicar diferentes variables continuas dependientes y sus variables explicativas considerando o no factores aleatorios. Sin embargo, en el cuarto capítulo, se llevó a cabo un

modelo de ecuaciones estructurales (SEM) para analizar las relaciones directas e indirectas entre las variables ambientales y la estructura de las comunidades. La gran mayoría de los análisis estadísticos, el procesamiento de datos, o el cálculo de los índices de diversidad se ha llevado a cabo utilizando el lenguaje de programación R (R Core Team, 2012) y una batería enorme de librerías específicas (FD, lme4, MuMIn, picante, vegan entre otras).

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Chapter 1

Determinants of high mountain plant diversity in the Chilean Andes: from regional to local spatial scales



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Abstract

Mountains are considered excellent natural laboratories for studying the determinants of plant diversity at contrasting spatial scales. To gain insights into how plant diversity is structured at different spatial scales, we surveyed high mountain plant communities in the Chilean Andes where man-driven perturbations are rare. This was done along elevational gradients located at different latitudes taking into account factors that act at small scales, including abiotic (potential solar radiation and soil quality) and biotic (species interactions) factors, and considering multiple spatial. Species richness, inverse of Simpson's concentration (D_{equiv}), beta-diversity and plant cover were estimated using the percentage of cover per species recorded in 34 sites in the different regions with contrasted climates. Overall, plant species richness, D_{equiv} and plant cover were lower in sites located at higher latitudes. We found a unimodal relationship between species richness and elevation and this pattern was constant independently of the regional climatic conditions. Soil quality decreased the beta-diversity among the plots in each massif and increased the richness, the D_{equiv} and cover. Segregated patterns of species co-occurrence were related to increases in richness, D_{equiv} and plant cover at finer scales. Our results showed that elevation patterns of plant diversity remained constant along the regions although the mechanisms underlying these diversity patterns may differ among climatic regions. Our results show that the patterns of plant diversity in alpine ecosystems respond to a series of factors (abiotic and biotic) that act jointly at different spatial scale determining the assemblages of local communities, but their importance can only be assessed using a multi-scale spatial approach.

Keywords: Alpine ecosystem; Beta-diversity; Community assembly; Ecological gradients; Species interactions; Summer drought

Introduction

Mountains are considered excellent natural laboratories for investigating how plant diversity is structured at contrasting spatial scales because extreme environmental conditions and steep climatic gradients are generated over short distances (Körner 2007; Sanders & Rahbek 2012). Spatial variation of environmental conditions varies with the grain size of investigation, and therefore, the plant community response to such abiotic heterogeneity depends on the spatial scale of observation (Wiens 1989; Leibold et al. 2004; Münkemüller et al. 2014). Then, mountains covering an ample region and alpine vegetation above the treeline are especially suited to infer how diversity patterns are conformed and what factors are critical at different spatial scales (Ricklefs 2008; Brooker et al. 2009; Götzenberger et al. 2012; Harmon & Harrison 2015).

At large-scales the description of latitudinal and elevational diversity patterns have occupied a central place and most studies reveal a decreasing trend in richness with latitude and altitude (Rohde 1992; Rahbek 1995; Rosenzweig 1995; Willig et al. 2003; Körner 2007; Rother et al. 2016). Although multiple theories have been proposed in order to explain these patterns, from available space with altitude to evolutionary history (McCain & Grytnes 2010), the intensification of environmental harshness via coldness with latitude and elevation have been frequently reported (Wright 1983; Currie et al. 2004). In any case the relationship between diversity and elevation varies from the expected decreasing monotonic to hump-backed with richness peaks at medium elevations (Rahbek 1995; Grytnes 2003; Nogués-Bravo et al. 2008). Such a variation could be explained by the fact that some gradients are very long and have dramatic changes in the vegetation types along them (high turnover rates along elevation within mountain ranges: 18), due to the historical human footprint and disturbances (Billings 1973; Olff & Ritchie 1998) or simply because the diversity patterns are compared at different spatial scale (Götzenberger et al. 2012). In other ocasiones, the effect exerted by other concomitant regional factors may reduce the species diversity in unexpected parts of the gradient. For example, the summer drought typical of Mediterranean climate regions is exacerbated at low elevations which may interact with the opposite cold stress gradient giving unexpected patterns (Cavieres et al. 2006; Giménez-Benavides et al. 2007; López-Angulo et al. 2018).

Factors operating at finer spatial scales may influence or alter those patterns found at larger spatial scales. For instance, environmental variations such as those induced by local topography (aspect or slope) at very fine scales may yield local differences in the length of the effective growing season due to different impact of solar radiation and duration of snow-free

periods (Kudo & Ito 1992; Bruun et al. 2006; Scherrer & Körner 2011; Graae et al. 2017). In addition, at this same fine scale, soil quality that allow greater primary productivity and plant diversity regardless of the overall habitat quality, could affect the large-scale patterns in diversity (Reynolds & Haubensak 2009; Eilts et al. 2011). However, the heterogeneity produced by the differences in nutrient availability varies across scales, and thus, soil conditions may affect diversity at large scales where species are filtered from the regional species pool to small scales where plant individuals interact (Olofsson et al. 2008).

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perimposed on this picture, biotic interactions such as competition and facilitation are critical determinants of plant diversity at the finest spatial scales in many ecosystems (Callaway 2007; Luzuriaga et al. 2011), including alpine plant communities (Choler et al. 2001; Cavieres & Badano 2009; Cavieres et al. 2014; Pescador et al. 2014). Specifically, the theoretical framework reveals an increase of the intensity of competition in benign environments with a clear dominance of a reduced group of species (Grime 1973), although competitive processes may promote species diversity by niche differentiation (Kikvidze et al. 2005). On the other hand, when environmental conditions become more stressful, facilitative interactions become more important (Callaway et al. 2002; Michalet et al. 2006). It has been shown that they can dampen the decreases in species richness acting as safety-net under stressful conditions (Cavieres et al. 2016). Thus, we might not find a monotonic decrease in diversity with elevation due to local conditions.

The Chilean Andes comprise a continuous and large north to south mountain system which leads a detailed survey of plant community diversity and determinants at multiple scales from latitude to microhabitat variation. Furthermore, in contrast to other mountain regions where the landscape and biota have been profoundly altered by human activities (Schwörer et al. 2015), thereby hindering the interpretation of diversity patterns (Billings 1973; Olff & Ritchie 1998), the Chilean Andes are characterized by a very low level of human-driven disturbances, especially in the southern region (Huber & Markgraf 2003). In addition, there are clear climate variations over a broad regional scale and it is possible to discern major differences along this mountain range. Taken all together the Chilean Andes constitutes a critical study area to gain insights into the determinants of high mountain plant diversity and to examine how plant diversity is structured at different spatial scales and if interactions between factors operating at different scales occur. Thus, we surveyed alpine plant communities along an elevational gradient at different latitudes (from -32°S to -52°S) comprising mountains with a Mediterranean-type climate where the summer drought is critical (Cavieres et al. 2006) to sub-Antarctic mountains where drought is negligible and summer temperature is low. Our main objectives were: (i) to determine the effect of elevation on taxonomic plant diversity (including alpha diversity as well as beta-diversity) and

plant cover at different spatial scales including some contrasted latitudes along the Chilean Andes; and (ii) to determine whether factors that act at small scales, including abiotic (potential solar radiation and soil quality) and biotic factors (species interactions), might modulate the effects of latitude and elevation on different components of plant diversity. We expected taxonomic diversity to decrease with elevation conforming a monotonic pattern, but with a sharp decline in the lower elevational limit in mountains with a Mediterranean-type climate due to the effect of the summer drought at lower elevations conforming a humpbacked structure (Cavieres et al. 2006).

Materials and methods

Study area

We selected three high mountain massifs over a long latitudinal gradient in the Chilean Andes (see Table 1, Fig 1): (1) Farellones located 40 km east of the city of Santiago; (2) Maule situated 100 km east of the city of Talca; and (3) Torres del Paine National Park located in sub-Antarctic Patagonia. In these three areas, the annual mean temperature is 5–6.5°C and precipitation is 900–950 mm. However, Farellones and Maule are influenced by a Mediterranean-type climate but the length of the summer drought is significantly longer at Farellones than at Maule (Sarricolea et al. 2017), and Torres del Paine NP has a sub-Antarctic climate without summer drought where the rainfall is distributed evenly throughout the year (Cavieres et al. 2002). Climatic data for each region are shown in Table 1.

Table 1 Geographic location, main climatic characteristics, treeline altitude, and treeline species for the study sites.

Study site	Location	Treeline altitude (m.a.s.l.)	Annual precipitation (mm)	Mean temperature (°C)	Treeline species
Farellones	33°2'S, 70°1'W	2200	9431	6.52	<i>Kageneckia angustifolia</i> (Rosaceae)
Maule	35°6'S, 70°3'W	1700	9003	53	<i>Nothofagus antarctica</i> (Nothofagaceae) <i>Austrocedrus chilensis</i> (Cupressaceae)
Torres del Paine	51°0'S, 73°0'W	500	9004	54	<i>Nothofagus pumilio</i> (Nothofagaceae)

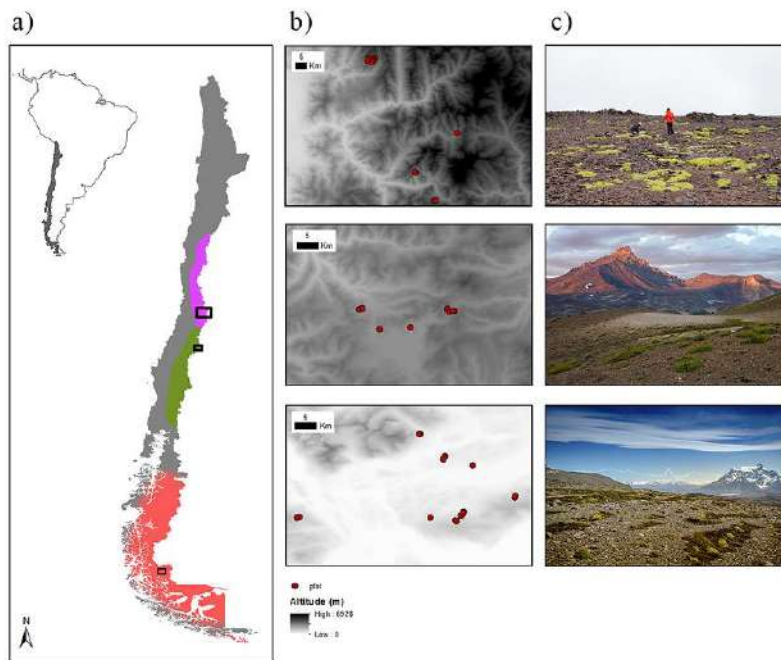
¹ Santibañez F, Uribe JM (1990) Atlas agroclimático de Chile: Regiones V y Metropolitana. Ministerio de Agricultura, Santiago, Chile.

² Cavieres LA, Peñaloza A, Arroyo MTK (2000) Altitudinal vegetation belts in the high-Andes of central Chile (33 S). *Rev Chil Hist Nat* 7:331–344.

³ Méndez E (2014) La vegetación de los altos Andes Centrales: Bardas Blancas-Paso Pehuenche (Malargüe, Mendoza, Argentina). *Boletín de la Sociedad Argentina de Botánica* 49:257–281.

⁴ Cavieres LA, Arroyo MTK, Peñaloza A, et al (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *J Veg Sci* 13:547–554.

Figure 1 Schematic of experimental design. (a) Locations of the three study areas (black quadrats) along the Chilean Andes. Colours (purple = Mediterranean-type climate region with a severe drought summer, green = Mediterranean-type climate region with a milder drought summer and red = sub-Antarctic region) represent three different climatic zones according to Sarricolea (2017); (b) plot distribution along the three areas; and (c) typical structure of the vegetation in each area



The vegetation above the treeline in these mountains is generally dominated by caespitose herbs (e.g. *Poa denudata* Steud), which are accompanied by other growth forms such as prostrate shrubs (e.g., *Berberis empetrifolia* Lam.), perennial forbs (e.g., *Phacelia secunda* J.F. Gmel. and *Nassauvia pyramidalis* Meyen), and cushion-like plants (e.g., *Azorella madreporica* Clos and *Laretia acaulis* (Cav.) Gillies & Hook). The treelines are formed by *Kageneckia angustifolia* D. Don (Rosaceae) in Farallones, *Austrocedrus chilensis* (D.Don) Pic-Serm. & Bizzarri (Cupressaceae) in Maule and *Nothofagus pumilio* (Poepp & Endl.) Krasser (Nothofagaceae) in Torres del Paine NP (see Table 1).

Field sampling

Field sampling was performed in the Mediterranean and sub-Antarctic climate regions during the summer in 2014 and 2015, respectively, in the summer season when the alpine plants were at their phenological peak. We sampled a total of 34 sites (11 in Farellones, 9 in Maule, and 14 in Torres del Paine) above the treeline selecting good representatives of alpine vegetation avoiding, rocks, screes, snow beds and disturbed areas, and covering the complete elevational range where the ecosystem occurs in each region. The sampled elevation ranged from 2477 to 3627 in Farellones, from 2064 to 2666 in Maule, and from 500 to 1050 m in Torres del Paine NP. In addition to the variation between regions and the complete altitudinal range taken in each mountain massif, at each site, the community structure was surveyed at three different spatial scales: (1) plot scale: one 20 m \times 20 m sampling plot per site attending to the macroclimate (via altitude) and microclimate (via slope and orientation); (2) quadrat scale: five 2.4 m \times 2.4 m quadrats were established within each plot, with one in each corner and a fifth in the centre corresponding to the scale in which in these communities the microsite variability (via soil heterogeneity) is better expressed; and (3) cell scale: the central quadrat was divided into 64 cells measuring 30 cm \times 30 cm, with a total of 2176 cells representing the scale in which plant to plant variations are critical (Fig 1). The percentage cover per species was sampled in each quadrat and in each cell. The plant cover per plot was calculated indirectly as the sum of the mean cover of each species in the five quadrats, where the plant cover in the central quadrat was estimated as the mean cover by each species in the 64 cells.

The cell data information obtained at the finest scale was used to estimate a checkerboard score (c-score: Stone & Roberts 1990), which quantifies the degree of spatial segregation for species co-occurrence, as an integrative estimate of plant to plant interactions. High c-score values denote that species pairs occur less frequently whereas low values indicate a tendency for species to aggregate spatially. The average size of the plant species in the community was around 15 cm in diameter, so the cell size appeared to be adequate for estimating real biotic interactions.

At each site (plot scale) we measured the elevation and slope aspect using a GPS (Garmin Colorado-300, Garmin Ltd, Olathe, USA), and a clinometer for the slope (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Elevation was standardized among the different mountain massifs in order to compare regions at various latitudes by subtracting the mean treeline elevation (determined using Google Earth images) from the plot elevation. Aspect

and slope values were used to calculate Gandullo's potential solar radiation coefficient (for details see: Gandullo 1974; López-Angulo et al. 2018)

In addition, at the quadrat scale we evaluated the soil quality by taking two soil cores with a diameter of 5 cm and depth of 10 cm from each corner-quadrat, with one from an open area and the other under the perennial and dominant plant. This yielded eight soil samples per plot. The soil samples were air dried for one month and then sieved through a 2-mm mesh. We assessed eight multi-functional ecosystem properties related to the cycling and storage of nutrients. In particular, we selected organic carbon (C), total nitrogen (N), available phosphorus (P), and potassium (K) as key nutrients related to primary productivity and the buildup of nutrient pools (Maestre et al. 2012b). These parameters are also surrogates for other forms of C, N, and P that are available to plants (Delgado-Baquerizo et al. 2013) and they can be treated as ecosystem functions related to soil fertility and primary productivity. Furthermore, we estimated the enzymatic activities of phosphatase and β -glucosidase, which are closely related to the microbial functionality and nutrient dynamics in soil. Soil organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid (Yeomans & Bremner 1988). Total N and available P were determined with a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in our laboratory after digestion with sulfuric acid and Kjeldahl's catalyst (Anderson & Ingram 1994). Potassium (K) was measured with the same analyzer system after shaking the soil samples with distilled water (1:5 ratio) for 1 h. Enzymatic activities were estimated using the methods described by Eivazi and Tabatabai (β -glucosidase; 1988) and Tabatabai and Bremner (acid phosphatase; 1969). The soil pH and electrical conductivity were measured in a soil and water suspension at a mass:volume ratio of 1:3 using a pH meter (GLP 21; Crison, Barcelona, Spain) and a conductivity meter (GLP 31; Crison, Barcelona, Spain), respectively. These variables were then averaged to obtain quadrat-level estimates based on the mean values determined in bare ground and vegetated areas, where they were weighted by the respective cover value in each quadrat. The centre quadrat value was estimated as the average of the four quadrats at each site. All of these soil variables are determinants of the functioning of ecosystems (Reiss et al. 2009; Jax 2010), so we calculated an ecosystem multi-functionality index (Maestre et al. 2012):

$$M_i = (\sum_{k=1}^n (x_{ki} - \mu_k) / \sigma_k) / n,$$

where M_i is the multi-functionality of plot i , n is the total number of soil parameters, x_{ki} is the value of parameter k in plot i , and μ_k and σ_k are the mean and standard deviation for each parameter k , respectively.

Note that for elevation, potential solar radiation and c-score we have a unique value for all scales, whereas that the soil quality values were particular for each quadrat and a unique value for each plot and all cells.

Diversity metrics

Species richness (S) was estimated as the number of plant species recorded in each sampling unit. We estimated the inverse of Simpson's concentration index (D_{equiv}) expressed as species richness equivalents as an additional alpha diversity measure according to Jost (2007):

$$D_{equiv} = 1 / \sum_i^S p_i^2,$$

where p_i is the cover proportion of species i and S is species richness. Cover data were square root-transformed before estimating D_{equiv} and the beta-diversity. We also measured beta-diversity to assess the non-directional variation in species composition across sampling units (Anderson et al. 2011). It was calculated as the mean pairwise Bray–Curtis floristic dissimilarities among samples (i.e., cells, quadrats and plots) within each group depending on the spatial scale (Anderson et al. 2011):

$$\bar{d} = \frac{1}{n-1} \sum_{i,j < i} d_{ij},$$

where n is the number of samples within each group and d_{ij} is the dissimilarity of a target sample i relative to another sample j . Thus, *plot beta-diversity* was the mean of all the pairwise dissimilarities between a target plot and the other plots within each of the three mountainous massifs. *Quadrat beta-diversity* was the mean of all the pairwise dissimilarities between a target quadrat and the other four quadrats within each of the 34 plots. *Cell beta-diversity* was the mean of all the pairwise dissimilarities between a target cell and the other 63 cells within each of the 34 centre quadrats. Finally, we measured plant cover (C, estimated as the sum of the cover by all species because the level of overlapping was very low in these plant communities) in each sampling unit as a surrogate for productivity.

Statistical analyses

The relationships between the standardized elevation, soil quality assessed by soil multifunctionality, potential solar radiation, biotic interactions (c-score), and the diversity metrics were analysed using generalized linear models (GLMs) at the plot scale, and with generalized linear mixed-effects models (GLMMs) at the quadrat and cell scales. The response of species richness to the predictors was evaluated with a Poisson error distribution and logarithmic link

function, and the response of D_{equiv} , beta-diversity and total plant cover were analysed using a Gaussian error distribution and identity link function.

We included region (i.e., Farellones, Maule, and Paine) as a fixed factor and plot as a random factor. Post hoc Tukey tests were performed to detect any significant differences among regions. The convenience of including the quadratic term of elevation and the interaction between elevation and massifs in the final models was evaluated using the AICc criterion. We checked for collinearity between the different environmental predictors using the variance inflation factor before implementing the models where they were below 2 in all cases, thereby indicating the absence of problems with co-linearity (Chatterjee & Hadi 2001). The normality of the standardized residuals was confirmed visually for all of the models. We square root-transformed the total plant cover in order to normalize the data before conducting the analyses. We estimated the statistical significance of each predictor using type-II analysis of variance. We calculated the total variance explained (R^2) by each GLM, and the conditional variance explained (R^2_c) by both fixed and random factors, as well as the marginal variance explained (R^2_m) by fixed factors for each GLMM using the MuMIn package. All of the statistical analyses were performed in R (v 3.2.4) using the lme4, car, and vegan packages (R Core Team, 2012).

Results

We recorded a total of 234 perennial plant species (a list of taxa are provided in S1 Table) in the 34 plots sampled in the three regions, with a total of 86, 86, and 118 species in the Farellones, Maule, and Torres del Paine NP, respectively. The species richness ranged from 12 to 50 species per plot, with a mean of 25.3 (± 10) plant species per plot (other mean of diversity metrics on three regions at three scales are provided in S2 Table). The most abundant species in Farellones were the cushion plants *Azorella madreporica* and *Laretia acaulis*, and graminoids such as *Rytidosperma pictum* and *Poa cf. denudata*. The graminoids comprising *Festuca acanthophylla* and *Poa cf. denudata* were dominant in the Maule region. Finally, in the sub-Antarctic region, the community was dominated by prostrate shrubs such as *Empetrum rubrum* at low elevations, whereas the higher zones were dominated by the cushion plant *Azorella monantha*.

The fitted GLMs and GLMMs explained a high proportion of the variance in the diversity component at all of the spatial scales considered (Table 2). There were significant relationships between all of the diversity metrics (i.e., species richness, D_{equiv} , beta-diversity, and total plant cover) and some of the considered predictors.

Table 2 Coefficients of the models (GLMs and GLMMs) examining the effects of environmental factors on the diversity indices at plot (20 x 20 m), and at quadrat (2.4 x 2.4 m) and cell (30 x 30 cm) scales.

	plot scale		quadrat scale		cell scale	
Species richness						
Intercept (Farellones)	3.08		2.27		0.48	
Massif		**		**		**
· Maule	0.24	ab	0.26	ab	0.63	ab
· Torres del Paine	0.29	b	0.43	b	0.63	b
Altitude	-0.12	**	-0.08		-0.02	
Altitude ²	-0.1	**				
Soil quality	0.2	***	0.14	**	0.32	**
Potential solar radiation	0.02		0.04		0.07	
C-score	0.07		0.19	***	0.45	***
R ²	0.89					
R ² m			0.39		0.41	
R ² c			0.7		0.56	
Inverse of Simpson's concentration						
Intercept (Farellones)	6.21		4.91		1.2	
Massif		**		**		***
· Maule	9.5	b	3.47	ab	1.55	b
· Torres del Paine	9.12	b	4.62	b	1.52	b
Altitude	-0.16		0.06		0.17	
Soil quality	3.8	*	0.99	*	0.69	**
Potential solar radiation	0.07		0.29		0.03	
C-score	1.32		1.88	**	1.01	***
R ²	0.5					
R ² m			0.32		0.38	
R ² c			0.67		0.53	
Beta-diversity						
Intercept (Farellones)	0.86		0.48		0.78	
Massif		***				
· Maule	-0.05	a	-0.01		0.04	
· Torres del Paine	-0.16	b	0.05		0.01	
Altitude	-0.04	**	0.03		0	

Soil quality	-0.04	*	0	-0.01
Potential solar radiation	0.01		-0.01	-0.03
C-score	-0.01		0.03	-0.06
R ²	0.67			
R ² m			0.18	0.16
R ² c			0.64	0.63
Plant cover				
Intercept (Farellones)	14.134		2.634	2.16
Massif		*		
· Maule	7.599	ab	-0.065	0.17
· Torres del Paine	15.836	b	0.242	-0.07
Altitude	-2.825	*	-0.239	0.03
Soil quality	9.081	**	0.286	* 0.43 *
Potential solar radiation	1.649		0.051	0.2
C-score	2.849		0.197	* 0.32 *
R ²	0.62			
R ² m			0.25	0.17
R ² c			0.39	0.33

Altitude²: the quadratic term of altitude.

R²: variance explained by each model. R²m: marginal variance explained by fixed factors. R²c: conditional variance explained by both fixed and random factors.

The significance is shown as *** P<0.001, ** P<0.005, * P<0.05.

Different letters within columns indicate significant differences (P< 0.05) between Farellones (a) and the other two regions according to Tukey's range test

At the plot scale, the quadratic relationship between elevation and species richness significantly improved the goodness of fit (AICc with quadratic term = 246.2 vs. without = 251.6). In addition, a more complex model including the interaction between elevation and massifs produced lower goodness of fit for all diversity metrics and scales. The negative quadratic relationship between elevation and species richness (Table 2) indicated that the number of species was higher toward intermediate elevations above the local treeline (500–700 m standardized elevation) with a decrease toward both edges, which was more pronounced toward the upper limit. This pattern was observed across the different regions despite species richness differed among them, being significantly higher in Torres del Paine than in Farellones (Table 2). Plant cover was negatively influenced by elevation at large scales (plot and quadrat scales; see Table 2), and plots in Torres del Paine had significantly higher plant cover than in Farellones.

D_{equiv} showed no statistically significant relationship with elevation. However, this index was significantly lower in Farellones than in the other two sites and the differences in D_{equiv} among regions were consistent at the three spatial scales considered (Table 2). Lastly, the beta-diversity exhibited a strong monotonic decrease with elevation at the plot scale but not at smaller ones (Table 2). The dissimilarity of the species composition (beta-diversity) among plots in each massif was significantly lower in Torres del Paine than in Farellones (Table 2).

We found a positive correlation between soil quality with species richness, the D_{equiv} and total plant cover. These relationships were maintained across the three spatial scales (Table 2). The beta-diversity decreased as soil quality increased at the plot scale (Table 2). There were no significant relationships between the diversity metrics and solar potential solar radiation (Table 2). The c-score index was positively associated with all the diversity metrics at fine spatial scales. Species richness, D_{equiv} , and plant cover increased as the frequency of species co-occurrence decreased at the quadrat and cell scales. Thus, a shift from an aggregated to segregated species co-occurrence pattern was observed with the increase in richness, D_{equiv} and plant cover (Table 2). In addition, species segregation was associated with decreases in the mean pairwise dissimilarities (beta-diversity) between cells.

Discussion

Our findings showed that the patterns of plant diversity in alpine ecosystems as hypothesized respond to a series of factors that mainly act at different spatial scale, i.e. climatic variation related to latitude, local variations in elevation and fine scale species interactions. Our results support the idea that the general variation of the elevational pattern in plant diversity can be due to the effect exerted by other concomitant factors which modify the primary patterns (Billings 1973; Rahbek 1995; Olff & Ritchie 1998; Grytnes 2003; Nogués-Bravo et al. 2008).

We found that species richness exhibited a unimodal relationship with the standardized elevation, with the maximum values at medium elevations within regions and the minimum values at both edges of the gradient. Surprisingly, this pattern was similar along the three massifs independently of the regional climatic conditions. The expected pronounced decrease in richness (and total plant cover) with altitude is due to the environmental severity (Rahbek 1995; Grytnes 2003), which increases with elevation because of coldness, short growing seasons, excessive radiation, and other factors (Körner 2007). This would induce a monotonic relationship, which is then modulated by other local factors to obtain a unimodal pattern. In our opinion, the factors responsible for generating this humped pattern differed among climates. For instance, high

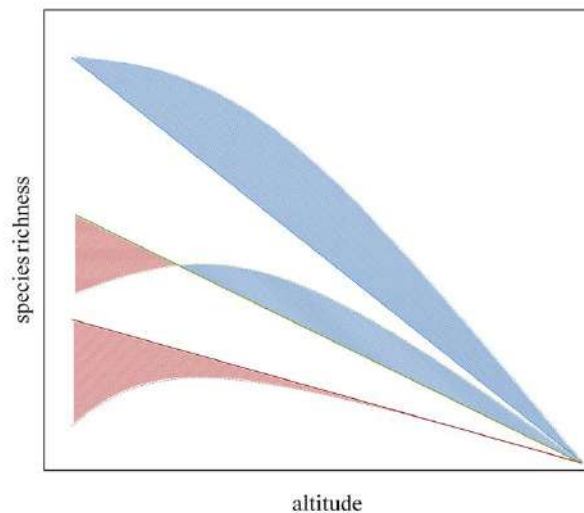
mountain Mediterranean-type massifs are characterized by summer drought at low elevations, which shortens the growing season (Cavieres et al. 2006). This implies that stress is intense at both ends of the elevational gradient with coldness at the highest elevations and drought at the lowest elevations, but more benign conditions at intermediate elevations (Mihoč et al. 2016) and therefore greater species richness. Some previous studies have suggested that water deficit is not a critical determinant of plant diversity in alpine habitats (Körner 2007) but our results in accordance with those obtained in Mediterranean regions (Cavieres et al. 2006; Giménez-Benavides et al. 2007; Reverter et al. 2010).

In the temperate sub-Antarctic Chilean Andes summer drought is practically negligible, thus the humped pattern in richness along elevation may be related to other mechanisms. The mass effect in an ecotone zone (Grytnes 2003), and the higher intensity of competitive exclusion (Grime 1973; Bruun et al. 2006) and disturbance (e.g. grazing; Grytnes et al. 2004) are factors that have been claimed to explain this pattern in other sub-Arctic mountains. However, we suggest this diversity pattern in Patagonian Andes is attributable to the effect of positive plant–plant interactions at intermediate elevations. It is known that facilitation by cushion plants and other nurse plants that dominate alpine ecosystems increases species richness at the entire community level (Cavieres & Badano 2009). Many studies have also shown that the magnitude of facilitation increases with the stress level (i.e., elevation), which could lead to an increase in richness as elevation increases (Cavieres et al. 2002; Callaway et al. 2002; Arroyo et al. 2003). Nonetheless, the intensity of the facilitative effect declines under extremely stressful conditions (Michalet et al. 2006), and thus a decay in species richness is expected at the uppermost limit of the elevational gradient due to coldness. If so, processes acting at very fine scale such as biotic interactions may modulate the effect of elevation on plant diversity. Our results suggest that different mechanisms can probably generate a very similar humpback pattern under contrasting climates and independently of the net differences in species richness along the Andes (Fig 2).

More direct evidences of the importance of biotic interactions in the structuration of diversity in these mountains were supported by the significant relation with plant diversity and also with productivity (i.e., total plant cover) at the quadrat and cell scales. We found that species segregation was related to higher richness, D_{equiv} , and total plant cover, thereby suggesting niche differences and spatial repulsion of species to avoid or reduce competition (MacArthur & Levins 1967; Chesson 2000; Silvertown 2004), which allowed more species to co-occur. However, the species co-occurrence patterns were not related to any of the plant diversity metrics at the plot scale. Therefore, the effects of species interactions could only be detected at the spatial scale

where individuals could potentially interact. However, it is worth mentioning that c-score is calculated as the mean average pairwise co-occurrence of all species, both the benefactor and beneficiary species, and thus, the expected facilitative effect that the benefactor nurses produce could become blurred.

Figure 2 Conceptual diagram showing the relationship between species richness and elevation. When the main environmental stressor is coldness (solid lines) in a long (red solid line) and short (green solid line) dry season in a Mediterranean-climate type mountain region and in a sub-Antarctic mountain region (blue solid line), and when summer drought (red dotted line), facilitation (blue dotted line), or both mechanisms (green dotted lines) act to modulate the original monotonic pattern. As a result, the richness decreases more markedly at low elevations in the Mediterranean-climate type region (red shaded area) whereas it increases more clearly at intermediate elevations in the sub-Antarctic region (blue shaded area).



An increase in harshness with elevation could be related to the parallel decrease in beta-diversity which reflects a species compositions of the assemblages more similar as elevation increased within each region. Other studies performed along elevational gradients also found a decrease in beta-diversity toward high elevations (Vázquez & Givnish 1998; Wang et al. 2002; Kraft et al. 2011). Our results suggest the prevalence of abiotic filters with altitude, thereby reducing the available species pool and leading to more homogeneous plant assemblages. In addition, soil quality that relates to critical ecosystem functions, such as carbon storage, productivity, and the buildup of nutrient pools (Maestre et al. 2012a), decreased the composition dissimilarity among plots in each massif. The differences in beta-diversity among communities may be related to the dominance of prostrate nurses and cushion-like shrubs such as *Azorella madreporica* and *Empetrum rubrum*. These species enhance soil quality because they increase

the availability of nutrients under their canopies (Jones et al. 1994; Badano & Cavieres 2006; Mihoč et al. 2016) generating fertility islands and increments in primary productivity (Escudero et al. 2004; Badano & Cavieres 2006). This implies that nurse species produce improvements of soil quality and amelioration of the extreme environmental conditions generating more stable and predictable conditions compared to the surrounding environment areas leading to species rich and constant assemblages, resulting again in a decrease in beta-diversity among plots (Kikvidze et al. 2015).

Our results showed that the patterns of taxonomic diversity in alpine ecosystems are related to both large-scale variables (climate estimated indirectly based on elevation and latitude) and small-scale variables (soil quality and biotic interactions), which jointly determine the assemblages of local communities and the patterning of diversity as a whole. Our findings demonstrate that a multi-scale approach is necessary to elucidate the mechanisms that shape alpine plant diversity over a large area because the effect of abiotic and biotic factors appeared to be patent only at particular scales. For example, elevation influenced the number of species and total plant cover, and these effects were clearly detectable at the plot scale, whereas the c-score affected diversity only at the finest scales (quadrat and cell). In addition, our results demonstrated that the patterns of taxonomic diversity with elevation remain constant along the regions in the Andes, although the mechanisms responsible for causing and maintaining these patterns differ among regions. The summer drought has important effects on the Andean communities in the central Mediterranean-type climate region of Chile (Cavieres et al. 2007; Giménez-Benavides et al. 2007) whereas facilitation may be critical in other regions. The combined effects of local biotic processes (such as facilitation) acting over large-scale abiotic gradients as well as regional factors determine the community assembly and the overall diversity patterns in stressed ecosystems.

Supporting Information

S1 Table. List of plant species occurring at each region.

S2 Table. The mean (\pm standard error) of all metrics of taxonomic community structure on three regions at plot, quadrat and cell scales.

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Declaration of authorship

JLA, AS, DP, LAC, and AE designed the study; AE and LAC provided logistic support in the field; JLA, DS, AS, MM, and AE collected the data; JLA analysed the data; JLA and AS wrote the manuscript with important contributions from all authors.

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Appendices

S1 Table: List of plant species occurring at each region

Family	Specie	Farellones	Maule	Torres del Paine
Rosaceae	<i>Acaena antarctica</i> Hook. f.			X
Rosaceae	<i>Acaena leptacantha</i> Phil.		X	
Rosaceae	<i>Acaena lucida</i> (Aiton) Vahl			X
Rosaceae	<i>Acaena macrocephala</i> Poepp.		X	
Rosaceae	<i>Acaena magellanica</i> (Lam.) Vahl			X
Rosaceae	<i>Acaena pinnatifida</i> Ruiz & Pav.	X	X	X
Rosaceae	<i>Acaena sericea</i> J. Jacq.			X
Rosaceae	<i>Acaena splendens</i> Hook. & Arn.	X		
Rosaceae	<i>Acaena</i> sp.			X
Fabaceae	<i>Adesmia boronioides</i> Hook. f.		X	
Fabaceae	<i>Adesmia capitellata</i> (Clos) Hauman	X		
Fabaceae	<i>Adesmia corymbosa</i> Clos			X
Fabaceae	<i>Adesmia glomerula</i> Clos	X	X	
Fabaceae	<i>Adesmia longiseta</i> DC.	X		
Fabaceae	<i>Adesmia lotoides</i> Hook. f.		X	X
Fabaceae	<i>Adesmia montana</i> Phil.	X		
Fabaceae	<i>Adesmia pumila</i> Hook. f.			X
Fabaceae	<i>Adesmia sandwithii</i> Burkart			X
Fabaceae	<i>Adesmia villosa</i> Hook. f.			X
Poaceae	<i>Agrostis</i> sp. 1			X
Poaceae	<i>Agrostis</i> sp. 2			X
Alstroemeriaceae	<i>Alstroemeria pallida</i> Graham	X		
Alstroemeriaceae	<i>Alstroemeria umbellata</i> Meyen	X		
Brassicaceae	<i>Alyssum alyssoides</i> L.			X
Fabaceae	<i>Anarthrophyllum desideratum</i> (DC.) Benth.			X
Ranunculaceae	<i>Anemone multifida</i> Poir.			X
Caryophyllaceae	<i>Arenaria serpens</i> Kunth		X	
Schoepfiaceae	<i>Arjona patagonica</i> Hombr. & Jacq. ex Decne			X
Plumbaginaceae	<i>Armeria maritima</i> (Mill.) Willd.		X	X
Asteraceae	<i>Asteraceae</i> sp.			X
Fabaceae	<i>Astragalus cruckshanksii</i> (Hook. & Arn.) Griseb.	X		
Fabaceae	<i>Astragalus palenae</i> (Phil.) Reiche			X
Fabaceae	<i>Astragalus</i> sp.	X		
Poaceae	<i>Avenella flexuosa</i> (L.) Drejer			X

Apiaceae	<i>Azorella filamentosa</i> Lam.			X
Apiaceae	<i>Azorella lycopodioides</i> Gaudich.			X
Apiaceae	<i>Azorella madreporica</i> Clos	X		
Apiaceae	<i>Azorella monantha</i> Clos		X	X
Apiaceae	<i>Azorella selago</i> Hook. f.			X
Apiaceae	<i>Azorella trifurcata</i> (Gaertn.) Pers.			X
Asteraceae	<i>Baccharis magellanica</i> (Lam.) Pers.			X
Asteraceae	<i>Baccharis neaei</i> DC.		X	
Ranunculaceae	<i>Barneoudia major</i> Phil.	X		X
Asteraceae	<i>Belloa chilensis</i> (Hook. & Arn.) J. Remy		X	
Berberidaceae	<i>Berberis empetrifolia</i> Lam.	X	X	X
Berberidaceae	<i>Berberis microphylla</i> G. Forst.			X
Blechnaceae	<i>Blechnum penna-marina</i> (Poir.) Kuhn			X
Apiaceae	<i>Bolax caespitosa</i> Hombr. & Jacq. ex Decne.			X
Apiaceae	<i>Bolax gummifera</i> (Lam.) Spreng.			X
Poaceae	<i>Bromus catharticus</i> Vahl	X		
Poaceae	<i>Bromus setifolius</i> J. Presl	X	X	X
Poaceae	<i>Bromus</i> sp.		X	
Montiaceae	<i>Calandrinia compacta</i> Barnéoud		X	
Calceolariaceae	<i>Calceolaria arachnoidea</i> Graham	X		
Calceolariaceae	<i>Calceolaria biflora</i> Lam.			X
Calceolariaceae	<i>Calceolaria corymbosa</i> Ruiz & Pav.	X		
Calceolariaceae	<i>Calceolaria filicaulis</i> Clos		X	
Calceolariaceae	<i>Calceolaria polyrhiza</i> Cav.		X	
Calceolariaceae	<i>Calceolaria uniflora</i> Lam.			X
Cyperaceae	<i>Carex andina</i> Phil	X	X	
Cyperaceae	<i>Carex aphylla</i> Kunth		X	
Cyperaceae	<i>Carex atropicta</i> Steud.		X	
Caryophyllaceae	<i>Cerastium arvense</i> L.	X	X	X
Asteraceae	<i>Chaetanthera euphrasioides</i> (DC.) F. Meigen	X	X	
Dennstaedtiaceae	<i>Cheilanthes glauca</i> (Cav.) Mett.	X		
Orchidaceae	<i>Chloraea magellanica</i> Hook. f.			
Asteraceae	<i>Chuquiraga oppositifolia</i> D. Don	X		
Montiaceae	<i>Cistanthe picta</i> (Gillies ex Arn.) Carolin		X	
Montiaceae	<i>Cistanthe</i> sp.	X		
Lamiaceae	<i>Clinopodium darwinii</i> (Benth.) Kuntze			X
Caryophyllaceae	<i>Colobanthus lycopodioides</i> Griseb.			X
Convolvulaceae	<i>Convolvulus demissus</i> Choisy		X	
Apiaceae	<i>Daucus montanus</i> Humb. & Bonpl. ex Spreng.			X
Apocynaceae	<i>Diplolepis nummulariifolia</i> (Hook. & Arn.)	X		

Rhamnaceae	<i>Discaria chacaye</i> (G. Don) Tortosa	X		
Brassicaceae	<i>Draba funiculosa</i> Hook. f.			X
Brassicaceae	<i>Draba gilliesii</i> Hook. & Arn.	X		
Brassicaceae	<i>Draba magellanica</i> Lam.			X
Poaceae	<i>Elymus magellanicus</i> (E. Desv.) A. Löve			X
Empetraceae	<i>Empetrum rubrum</i> Vahl ex Willd.			X
Ephedraceae	<i>Ephedra chilensis</i> C. Presl		X	X
Ephedraceae	<i>Ephedra frustillata</i> Miers			X
Asteraceae	<i>Erigeron andicola</i> DC.	X	X	X
Asteraceae	<i>Erigeron leptopetalus</i> Phil.		X	X
Asteraceae	<i>Erigeron myosotis</i> Pers.		X	X
Escalloniaceae	<i>Escallonia rubra</i> (Ruiz & Pav.) Pers.			X
Euphorbiaceae	<i>Euphorbia collina</i> Phil.	X	X	X
Poaceae	<i>Festuca acanthophylla</i> E. Desv.		X	
Poaceae	<i>Festuca gracillima</i> Hook. f.			X
Poaceae	<i>Festuca magellanica</i> Lam.		X	
Poaceae	<i>Festuca pyrogea</i> Speg.			X
Poaceae	<i>Festuca</i> sp.		X	
Rubiaceae	<i>Galium antarcticum</i> Hook. f.			X
Rubiaceae	<i>Galium eriocarpum</i> Bartl. ex DC.		X	
Asteraceae	<i>Gamochaeta nivalis</i> Cabrera			X
Asteraceae	<i>Gamochaeta</i> sp.		X	
Ericaceae	<i>Gaultheria caespitosa</i> Poepp. & Endl.			X
Geraniaceae	<i>Geranium sessiliflorum</i> Cav.	X		X
Gunneraceae	<i>Gunnera magellanica</i> Lam.			
Ranunculaceae	<i>Hamadryas delfinii</i> Phil. ex Reiche			X
Asteraceae	<i>Haplopappus anthylloides</i> Meyen & Walp.	X	X	
Poaceae	<i>Hordeum comosum</i> J. Presl	X	X	X
Asteraceae	<i>Hypochaeris clarionoides</i> (J. Remy) Reiche	X		
Asteraceae	<i>Hypochaeris incana</i> (Hook. & Arn.) Macloskie			X
Asteraceae	<i>Hypochaeris tenerifolia</i> (J. Remy) Dusén			X
Juncaceae	<i>Juncaceae</i> sp.			X
Juncaceae	<i>Juncus balticus</i> Willd.		X	
Verbenaceae	<i>Junellia tridens</i> (Lag.) Moldenke			
Apiaceae	<i>Laretia acaulis</i> (Cav.) Gillies & Hook.	X	X	
Liliaceae	<i>Latace andina</i> (Poepp.) Sassone	X		
Fabaceae	<i>Lathyrus magellanicus</i> Lam.			X
Asteraceae	<i>Leucheria leontopodioides</i> (Kuntze) K. Schum.	X		X
Asteraceae	<i>Leucheria lithospermifolia</i> (Less.) Reiche		X	
Asteraceae	<i>Leucheria millefolium</i> Dusén & Skottsb.		X	

Asteraceae	<i>Leucheria senecioides</i> Hook. & Arn.	X		
Asteraceae	<i>Leucheria viscida</i> (Bertero ex Colla) Crisci	X		
Loasaceae	<i>Loasa pinnatifida</i> Gillies ex Arn.	X		
Loasaceae	<i>Loasa sigmoidea</i> Urb. & Gilg	X	X	
Juncaceae	<i>Luzula alopecurus</i> Desv.	X	X	X
Juncaceae	<i>Luzula parvula</i> Barros	X	X	
Juncaceae	<i>Luzula racemosa</i> Desv.		X	
Juncaceae	<i>Luzula</i> sp.			X
Juncaceae	<i>Marsippospermum reichei</i> Buchenau			X
Montiaceae	<i>Melosperma andicola</i> (Gillies) Benth.	X		
Brassicaceae	<i>Menonvillea cuneata</i> (Gillies & Hook.) Rollins		X	
Brassicaceae	<i>Menonvillea scapigera</i> (Phil.) Rollins	X		
Brassicaceae	<i>Microsteris gracilis</i> (Hook.) Greene	X		
Montiaceae	<i>Montiopsis andicola</i> (Gillies) D.I. Ford	X		
Montiaceae	<i>Montiopsis gayana</i> (Barnéoud) D.I. Ford		X	
Montiaceae	<i>Montiopsis potentilloides</i> (Barnéoud) D.I. Ford	X		
Montiaceae	<i>Montiopsis</i> sp.		X	
Montiaceae	<i>Montiopsis potentilloides</i> (Barnéoud) D.I. Ford	X		
Apiaceae	<i>Mulinum spinosum</i> (Cav.) Pers.		X	X
Asteraceae	<i>Mutisia linearifolia</i> Cav.	X		
Asteraceae	<i>Mutisia sinuata</i> Cav.	X		
Boraginaceae	<i>Myosotis</i> sp.			X
Asteraceae	<i>Nardophyllum bryoides</i> (Lam.) Cabrera			X
Asteraceae	<i>Nassauvia aculeata</i> (Less.) Poepp. & Endl.			X
Asteraceae	<i>Nassauvia darwinii</i> (Hook. & Arn.) O. Hoffm.			X
Asteraceae	<i>Nassauvia digitata</i> Wedd.		X	
Asteraceae	<i>Nassauvia dusenii</i> O. Hoffm.			X
Asteraceae	<i>Nassauvia glomerata</i> (Gillies ex D. Don) Wedd.	X	X	
Asteraceae	<i>Nassauvia lagascae</i> (D. Don) F. Meigen		X	
Asteraceae	<i>Nassauvia maeviae</i> Cabrera			X
Asteraceae	<i>Nassauvia pygmaea</i> Hook.f.			X
Asteraceae	<i>Nassauvia pyramidalis</i> Meyen		X	
Asteraceae	<i>Nassauvia revoluta</i> D. Don	X	X	
Calyceraceae	<i>Nastanthus scapigerus</i> (J. Remy) Miers	X	X	
Calyceraceae	<i>Nastanthus ventosus</i> (Meyen) Miers	X	X	X
Brassicaceae	<i>Noccaea magellanica</i> (Comm. ex Poir.) Holub	X	X	
Nothofagaceae	<i>Nothofagus pumilio</i> (Poepp. & Endl.) Krasser			X
Onagraceae	<i>Oenothera magellanica</i> Phil.			X
Iridaceae	<i>Olsynium biflorum</i> (Thunb.) Goldblatt			X
Iridaceae	<i>Olsynium frigidum</i> (Poepp.) Goldblatt	X		

Iridaceae	<i>Olsynium junceum</i> (E. Mey. ex C. Presl) Goldblatt	X		
Iridaceae	<i>Olsynium scirpoideum</i> (Poepp.) Goldblatt	X	X	
Brassicaceae	<i>Onuris papillosa</i> O.E. Schulz			X
Rubiaceae	<i>Oreopolus glacialis</i> (Poepp.) Ricardi	X		X
Asteraceae	<i>Oriastrum lycopodioides</i> (J. Remy) Wedd.		X	
Asteraceae	<i>Oriastrum pusillum</i> Poepp. & Endl.		X	X
Apiaceae	<i>Osmorhiza chilensis</i> Hook. & Arn.	X		
Oxalidaceae	<i>Oxalis adenophylla</i> Gillies ex Hook. & Arn.		X	
Oxalidaceae	<i>Oxalis compacta</i> Gillies ex Hook. & Arn.	X		
Oxalidaceae	<i>Oxalis enneaphylla</i> Cav.			X
Oxalidaceae	<i>Oxalis laciniata</i> Cav.			X
Oxalidaceae	<i>Oxalis penicillata</i> Phil.	X		
Oxalidaceae	<i>Oxalis squamata</i> Zucc.	X		
Poaceae	<i>Pappostipa chrysophylla</i> (E. Desv.) Romasch.		X	X
Asteraceae	<i>Perezia carthamoides</i> (D. Don) Hook. & Arn.	X		
Asteraceae	<i>Perezia linearis</i> Less.			X
Asteraceae	<i>Perezia lyrata</i> (J. Remy) Wedd.		X	
Asteraceae	<i>Perezia pilifera</i> (D. Don) Hook. & Arn.	X		X
Ericaceae	<i>Pernettya prostrata</i> (Cav.) DC.			X
Caryophyllaceae	<i>Petrorhagia dubia</i> (Raf.) G. López & Romo			X
Boraginaceae	<i>Phacelia secunda</i> J.F. Gmel.	X	X	X
Poaceae	<i>Phleum alpinum</i> L.			
Plantaginaceae	<i>Plantago hispidula</i> Ruiz & Pav.		X	
Plantaginaceae	<i>Plantago lanceolata</i> L.			X
Poaceae	<i>Poa alopecurus</i> (Gaudich. ex Mirb.) Kunth			X
Poaceae	<i>Poa</i> gr. <i>denudata</i> 1	X	X	
Poaceae	<i>Poa</i> gr. <i>denudata</i> 2	X	X	
Poaceae	<i>Poa</i> gr. <i>denudata</i> 3	X		
Poaceae	<i>Poa lanuginosa</i> Poir. (Phil.) Giussani & Soreng			X
Poaceae	<i>Poa spiciformis</i> (Steud.) Hauman & Parodi			X
Polygalaceae	<i>Polygala salasiana</i> Gay		X	
Apiaceae	<i>Pozoa coriacea</i> Lag.	X	X	
Schoepfiaceae	<i>Quinchamalium chilense</i> Molina	X	X	
Liliaceae	<i>Ribes magellanicum</i> Poir.			X
Polygonaceae	<i>Rumex acetosella</i> L.			X
Poaceae	<i>Rytidosperma lechleri</i> Steud.	X		
Poaceae	<i>Rytidosperma pictum</i> (Nees & Meyen) Nicora	X		
Poaceae	<i>Rytidosperma virescens</i> (E. Desv.) Nicora	X	X	X
Apiaceae	<i>Sanicula graveolens</i> Poepp. ex DC.	X	X	
Saxifragaceae	<i>Saxifraga magellanica</i> Poir.			X

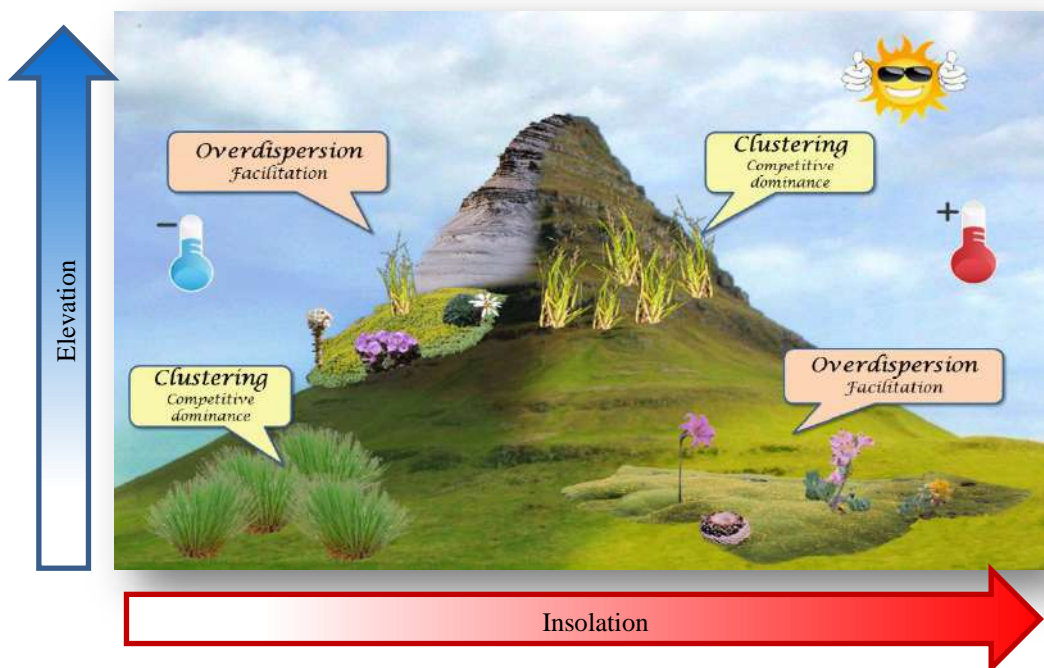
Lamiaceae	<i>Scutellaria nummulariifolia</i> Hook. f.			X
Asteraceae	<i>Senecio alloephyllus</i> O. Hoffm.			X
Asteraceae	<i>Senecio argyreus</i> Phil.			X
Asteraceae	<i>Senecio clarioneifolius</i> J. Rémy	X		
Asteraceae	<i>Senecio crithmoides</i> Hook. & Arn.		X	
Asteraceae	<i>Senecio francisci</i> Phil.	X		
Asteraceae	<i>Senecio gnidioides</i> Phil.			X
Asteraceae	<i>Senecio laseguii</i> Hombr. & Jacquinot			X
Asteraceae	<i>Senecio looseri</i> Cabrera	X		
Asteraceae	<i>Senecio pachyphyllos</i> J. Remy		X	
Asteraceae	<i>Senecio patagonicus</i> Hook. & Arn.			X
Asteraceae	<i>Senecio peteroanus</i> Phil.	X	X	
Asteraceae	<i>Senecio</i> sp. 1			X
Asteraceae	<i>Senecio</i> sp. 2			X
Asteraceae	<i>Senecio</i> sp. 3			X
Asteraceae	<i>Senecio</i> sp. 4		X	
Asteraceae	<i>Senecio subumbellatus</i> Phil.		X	
Asteraceae	<i>Senecio vaginifolius</i> Sch. Bip.			X
Caryophyllaceae	<i>Silene chilensis</i> (Naudin) Bocquet		X	
Caryophyllaceae	<i>Silene magellanica</i> (Desr.) Bocquet			X
Iridaceae	<i>Sisyrinchium arenarium</i> Poepp.	X	X	X
Iridaceae	<i>Solenomelus segethii</i> (Phil.) Kuntze	X	X	
Lamiaceae	<i>Stachys grandidentata</i> Lindl.	X		
Asteraceae	<i>Taraxacum gilliesii</i> Hook. & Arn.			X
Asteraceae	<i>Taraxacum officinale</i> G. Weber ex F.H. Wigg.	X		
Poaceae	<i>Trisetum preslei</i> (Kunth) E. Desv.	X	X	
Poaceae	<i>Trisetum spicatum</i> (L.) K. Richt.	X	X	X
Poaceae	<i>Trisetum</i> sp.			X
Liliaceae	<i>Tristagma nivale</i> Poepp. f.			X
Asteraceae	<i>Tristaria</i> sp.		X	
Tropaeolaceae	<i>Tropaeolum polyphyllum</i> Cav.	X		
Valerianaceae	<i>Valeriana carnosa</i> Sm.			
Valerianaceae	<i>Valeriana philippiana</i> Briq.			X
Fabaceae	<i>Vicia bijuga</i> Gillies ex Hook. & Arn.		X	X
Violaceae	<i>Viola atropurpurea</i> Leyb.	X		
Violaceae	<i>Viola cotyledon</i> Ging.		X	
Violaceae	<i>Viola maculata</i> Cav.			X
Violaceae	<i>Viola philippii</i> Leyb.	X		

S2 Table: The mean (\pm standard error) of all diversity metrics on three regions at plot, quadrat and cell scales.

Region	Species richness	Inverse of Simpson's concentration index	Beta-diversity	Plant cover
plot scale				
Farellones	20.82 \pm 1.69	8.97 \pm 1.23	0.82 \pm 0.02	20.00 \pm 2.35
Maule	22.33 \pm 2.67	11.80 \pm 1.73	0.87 \pm 0.02	14.51 \pm 2.64
Torres del Paine	29.80 \pm 2.80	15.69 \pm 1.75	0.72 \pm 0.02	29.79 \pm 4.56
quadrat scale				
Farellones	11.05 \pm 0.58	5.86 \pm 0.37	0.47 \pm 0.15	20.00 \pm 1.75
Maule	11.78 \pm 0.71	7.25 \pm 0.47	0.47 \pm 0.10	14.51 \pm 2.00
Torres del Paine	16.94 \pm 1.01	9.40 \pm 0.62	0.52 \pm 0.13	32.17 \pm 3.49
cell scale				
Farellones	2.37 \pm 0.07	1.92 \pm 0.05	0.75 \pm 0.16	27.30 \pm 1.03
Maule	2.40 \pm 0.08	1.82 \pm 0.06	0.82 \pm 0.15	16.07 \pm 0.96
Torres del Paine	4.17 \pm 0.12	2.74 \pm 0.08	0.80 \pm 0.18	19.14 \pm 0.85

Chapter 2

Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean-type climate mountains in the Andes



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Abstract

Questions: How do phylogenetic and functional trait dispersions respond to multiple abiotic gradients? Are functional trait and phylogenetic dispersions coupled across different spatial scales? Does phylogenetic signal on functional trait data help to elucidate the degree to which phylogenetic information is providing novel information?

Location: The study was performed in three massifs of the Mediterranean-type climate zone of the high Andes of central Chile.

Methods: We sampled plant species composition in 20 alpine sites above the treeline at three different spatial scales: plot (20 x 20m), subplot (2.4 x 2.4 m) and cell (30 x 30 cm). Functional and phylogenetic mean pairwise distances (MPD) calculated using data on six functional traits (maximum plant height, plant size, leaf area, specific leaf area, leaf dry matter content and leaf thickness) and a molecular phylogeny (rbcL and matK) were compared to the patterns expected under a null model to characterize the functional and phylogenetic dispersion along interacting elevation and potential solar radiation gradients.

Results: Our results show that functional and phylogenetic dispersion were related and influenced by potential solar radiation, but the effect of this factor varied with elevation. Overdispersion was found in the most stressful sites while clustering was observed where the conditions were milder, suggesting a relevant role of facilitation and competitive interactions, respectively. While Blomberg's K statistic indicated no phylogenetic signal for the studied plant traits, Pagel's λ indicated phylogenetic signal, but not of strong intensity (< 1), suggesting that the correlation between the functional and phylogenetic diversities was low and that additional unmeasured traits with phylogenetic signal were likely to be important in determining the structure of the studied communities.

Conclusions: Our results support the hypothesis that biotic interactions modulated by environmental conditions are important for alpine plant community assembly. Moreover, they reinforce the notion that multiple processes shape community structure, and this can be elucidated by examining interacting environmental gradients such as elevation and potential solar radiation, and taking into account multiple spatial scales. Our results reinforces the use of both functional and phylogenetic diversities simultaneously and discourages the use of the phylogenetic diversity as a surrogate of the functional structure.

Introduction

Disentangling the drivers that determine community assembly and diversity patterns remains a critical topic in ecology (Lortie et al. 2004; Götzenberger et al. 2012; HilleRisLambers et al. 2012). The current paradigm suggests the existence of a complex balance between stochastic and deterministic processes (Chase et al. 2011) leaving detectable spatial signals on community properties (McIntire & Fajardo 2009; Pavoine et al. 2011). Species interactions (both positive and negative) and environmental filtering are considered the most relevant deterministic drivers of community assembly leaving observable imprints on the spatial structure (Wang et al. 2015; Chacón-Labella et al. 2016).

Critical for an appropriate understanding of the balance between deterministic and stochastic processes in community assembly is our ability to quantify the similarity of species, or the role played by each species, in the assembly process. The unrealistic assumption that all species are equivalent independently of the role that each of them plays in the field implicitly used when evaluating patterns of taxonomic diversity, has led to the evaluation of the functional similarity among species and their phylogenetic relatedness (Kraft et al. 2007; Cadotte et al. 2009) as indicators of the overall ecological similarity among species. For instance, the functional approach infer assembly processes by comparing the distribution of plant functional traits within communities with those expected from null assemblages. There, abiotic filtering and competitive exclusion lead to clustering of functional traits compared to null models (Diaz et al. 1998). Conversely, niche differentiation and facilitative interactions produce an overdispersion of functional traits (Valiente-Banuet & Verdú 2007; Kraft et al. 2008).

Although trait-based plant community ecology offers a valuable conceptual framework (Shipley et al. 2016) and the number of papers published using this approach has grown exponentially (Escudero & Valladares 2016), there are some limitations. One of these limitations is the reduced set of traits that are often measured. Sometimes, important, but unmeasured aspects of plant functioning are not considered (Shipley et al. 2016). For this reason, phylogenetic data are often used as a proxy for the functional similarity of species in communities (Kraft et al. 2007). This phylogenetic approach is rooted in the simple idea that closely related species are ecologically/functionally more similar than more distant relatives (Burns & Strauss 2011). This relationship can be estimated using measures of phylogenetic signal on traits (Blomberg et al. 2003). In those cases where there is a strong signal, phylogenetic dispersion should reflect the functional dispersion since closely related species are expected to

have similar trait values due to common ancestry (Cavender-Bares et al. 2004; Swenson et al. 2007; Swenson & Enquist 2009). However, when trait distribution has a low phylogenetic signal, phylogenetic data can provide information about unmeasured traits (Swenson & Enquist 2009; Peres-Neto & Kembel 2015).

Despite the large amount of work quantifying the functional and phylogenetic structure of communities over the past decade, a general picture regarding the processes driving assembly remains unclear. Although discrepancies between trait and phylogenetic dispersion are common (Swenson et al. 2007; Swenson & Enquist 2009), discrepant functional or phylogenetic patterns have also been found in communities due to differences in the spatial and temporal scales utilized (Swenson et al. 2006; Götzenberger et al. 2012). An explanation for seemingly conflicting results could be that different processes may be simultaneously operating at different scales, in response to different environmental factors (Grime 2006; Vonlanthen et al. 2006), producing opposing effects (see Soliveres et al. 2012) sometimes difficult to predict.

Functional trait dispersion is frequently considered as an integrated response to single environmental gradients or to multiple, but independent gradients (de Bello et al. 2013; Schöb et al. 2013; Dainese et al. 2015). However, multiple gradients are rarely considered simultaneously (e.g. Swenson & Enquist 2007). To know how and to what extent communities respond to interacting gradients could explain discrepancies when functional and phylogenetic structures have been explored in modeled plant assemblages (May et al. 2013) or along a complete range of spatial scales (Chacón-Labela et al. 2016). For instance, hydraulic conductance and photosynthesis are governed by water availability, water potential gradients and temperature, which ultimately result from an interaction between precipitation and temperature and not from each factor independently (Thornthwaite 1948). Thus, it is important to evaluate the complementarity between functional and phylogenetic approaches by exploring whether or not they are redundant along complex and simultaneous environmental gradients and considering different spatial scales.

Here, we assessed plant functional trait and phylogenetic dispersion along interacting elevation and potential solar radiation gradients controlling the effect of the soil fertility and species spatial aggregation. This was done across multiple-spatial scales -plot (20 x 20m), subplot (2.4 x 2.4 m) and cell (30 x 30 cm)- to provide insights into the processes that drive community assembly. The study was performed in mountains of the Mediterranean-type climate zone of the central Chilean Andes. These habitats are an ideal model system to our objectives as they cover a wide elevational gradient where multiple abiotic variables exhibit gradients that are

not co-linear (Pescador et al. 2015). Our specific objectives were (1) to quantify phylogenetic and functional trait dispersion in communities along multiple abiotic gradients; (2) to determine the degree to which functional trait and phylogenetic dispersion are coupled across different spatial scales; and (3) to evaluate phylogenetic signal on functional traits to help to elucidate the degree to which phylogenetic information is providing novel information.

Methods

Study area

This study was conducted in three Andean massifs of the Mediterranean-type climate zone of central Chile (Appendix S1) nearly covering the complete latitudinal gradient where this ecosystem occurs in South America; more than 400 kilometers long: (1) Farellones 40 km east of the city of Santiago; (2) Morado at the Maipo River Basin, 80 km south-east of the city of Santiago; and (3) Maule, 100 km east of the city of Talca (see Table 1). The elevation in our study ranges from 2064 to 3627 m.a.s.l. The inter-annual rainfall variability is extremely high. Precipitation mainly occurs as snow during the winter. Summers are extremely dry and the summer drought increases at lower elevations.

Table 1. Geographic location, main climatic characteristics, treeline elevation and treeline species of the studied sites.

Study site	Location	Annual precipitation (mm)	Mean temperature (°C)	Treeline elevation (m a.s.l.)	Treeline species
Farellones	33°20'S, 70°14'W	9431	6.52	2200	<i>Kageneckia angustifolia</i> (Rosacea)
Morado	33°46'S, 70°01'W	11724	8.73	2100	<i>Kageneckia angustifolia</i> (Rosacea)
					<i>Nothofagus antarctica</i> (Nothofagaceae)
Maule	35°58'S, 70°30'W	9005	55	1700	<i>Austrocedrus chilensis</i> (Cupressaceae)

¹Santibañez & Uribe (1990), ²Cavieres, Peñaloza & Arroyo (2000), ³Fabres (2009), ⁴Muñoz-Schiciu, Moreira-Muñoz & Villagrán (2000) and ⁵Méndez (2014).

Vegetation above the treeline in the Andes of Central Chile generally comprises prostrate shrubs (e.g. *Berberis empetrifolia* Lam.) and some annual species (e.g. *Chaetanthera euphrasioides* (DC.) F. Meigenat) at lower elevations, while at the higher elevation the community is dominated by cushion-like plants (e.g. *Azorella madreporica* Clos) and caespitose and rosette-forming perennial herbs (e.g. *Nassauvia pyramidalis* Meyen) (Cavieres et al. 2000).

Experimental design

In the summer of 2014, we sampled 20 alpine sites above the treeline selecting representative patches of alpine vegetation (Appendix S1) avoiding screes, rocks and wet habitats. Vegetation was sampled at three different spatial scales (Appendix S1): 1) Plot scale: at each site, we established a 20 m x 20 m plot in a representative area with homogeneous vegetation and avoiding, rocks, screes, snow beds or humid depressions; 2) Subplot scale: five 2.4 m x 2.4 m subplots were established within each plot, one in each corner and a fifth in the center; 3) Cell scale: the central subplot was thoroughly divided into 64 cells of 30 cm x 30 cm. We registered the cover of any plant species at each subplot and at each cell. Finally, the species cover at the plot scale was calculated as the average of the covers of each species in the five subplots.

We characterized the environment at each plot by determining several variables. Specifically, the elevation and aspect were obtained by using a GPS (Garmin Colorado-300, Garmin Ltd., Olathe, USA) and the slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). As the three zones are in different latitudes and this factor may influence community assembly, elevation was standardized by subtracting the treeline altitude from plot elevation. Local treeline limits were identified by Google Earth and averaging the elevation of conspicuous trees in the area. Aspect and slope values were used to calculate Gandullo's potential solar radiation coefficient (Gandullo 1974):

$$Gla = \sin i \cdot \cos p - \cos \alpha \cdot \cos i \cdot \sin p$$

$$Glb = \sin i \cdot \cos p + \cos \alpha \cdot \cos i \cdot \sin p$$

Where Gla is the potential solar radiation calculated in north-facing sites and Glb in south-facing sites, i is the solar incidence angle (i.e. 90° - latitude), p is the slope, α is the angle formed by the aspect and 0° for Gla and the aspect and 180° for Glb .

To assess soil fertility, two soil samples (5 cm in diameter and 10 cm deep) were collected at each corner-subplot; one in an open area and the other under a vegetated patch with the dominant species in the community. Soil samples were air dried for one month and sieved through a 2 mm mesh and eight parameters of functional ecosystem properties related to the cycling and storage of nutrients were estimated. Specifically, we estimated organic carbon (C), total nitrogen (N), available phosphorus (P) and potassium (K) as key nutrients related to primary productivity and the buildup of nutrient pools (Maestre et al. 2012). In addition, we estimated Phosphatase and β -glucosidase soil enzymatic activities that are tightly related to soil microbial functionality and rapid nutrient dynamics. Further details regarding the estimation of soil properties are provided in Appendix S2. The two soil variables per subplot were used to obtain a subplot-level estimate of soil parameters. This was done by weighting the soil values using the mean cover observed for bare ground and vegetated areas in the subplot. The center subplot value was estimated as the average of four subplots at each site. With all of them we calculated the multifunctionality index proposed by Maestre et al. (2012) as an indicator of soil fertility.

Phylogenetic analysis

To estimate the phylogenetic diversity and relatedness, a molecular phylogeny was generated for the community using two barcoding loci (rbcL and matK). Phylogenetic analysis are explained in Appendix S3.

Plant functional traits

During the austral summer season of 2015 functional traits were measured for 71 species, which represented at least 80% of the cumulated cover of each subplot (Borgy et al. 2017). We measured six plant functional traits which *a priori* are expected to respond to the environmental conditions along the elevation gradient. Maximum plant height (MPH) represents a trade-off between competitive vigor (Cornelissen et al. 2003) and protection by snow cover (Körner 2003); plant size (SI) as a surrogate of accumulated resources (Pescador et al. 2015), leaf area (LA) is related to cold stress and drought (Cornelissen et al. 2003); specific leaf area (SLA) is related to growth and photosynthetic capacity (Cornelissen et al. 2003); leaf dry matter content (LDMC) is related to investment in leaf tissues, storage and structural defense (Cornelissen et al. 2003); and leaf thickness (LT) that is related to nutrient cycling and resistance to wind (Choler 2005). All these traits were measured using standardized protocols (Cornelissen et al. 2003) with the exception of plant size (SI: Pescador et al. 2015), which was calculated as $SI = \pi \cdot L \cdot S/4$, where L is the longest diameter and S is the shorter diameter perpendicular to the former one.

Diversity estimates and statistical analyses

Functional and phylogenetic mean pairwise distances (MPD) weighted by cover values from each sampling unit (three scales) were compared to the patterns derived from a null model. We utilized an independent swap null modeling approach because species abundance was not correlated with traits and it was not phylogenetically structured (Blomberg's $K < 0.001$, $P = 0.11$ and Pagel's $\lambda = 0.089$, $P = 0.54$) (Blomberg et al. 2003; Hardy 2008). This null model randomizes the site-by-species community data matrix which maintains the observed species richness of communities (i.e. row sums) and the occupancy rates of species across the study system (i.e. column sums). We generated 999 random community matrices using the independent swap. The functional or phylogenetic dispersion we used to calculate the corresponding standardized effect size SES (SES: Gotelli & McCabe 2002) where positive values indicated more observed diversity than expected (i.e. overdispersion) and negative values indicated less diversity than expected (i.e. clustering). It is worth noting that the dispersion values were considered emergent properties of the realized assemblage at each spatial scale independently of the fact they were significant or not in relation to a specific null model. Before analysis, the traits were log-transformed to reach normality when necessary and centered by their standard deviation.

We tested whether functional and phylogenetic diversity provided similar patterns due to phylogenetic signal (i.e. tendency for closely related species to be more similar) assessed with the K statistic of Blomberg and with Pagel's λ using a Brownian motion model of trait evolution (Pagel 1999; Blomberg et al. 2003).

The effects of two coincident abiotic gradients, elevation, potential solar radiation and their interaction, on the functional and phylogenetic dispersion were analyzed using linear models at the plot scale and generalized linear mixed models (GLMM) at subplot and cell scales. Zone (massif) and plot were considered a fixed effect and a random effect respectively to take in account the longitudinal dependences of the data.

In addition, we considered two other fixed predictors, soil fertility and the biotic interactions measured as the checkerboard score (C-score: Stone & Roberts 1990) in order to have a statistical control of these sources of community variation. The C-score calculated with the cell data, gives an estimate of the degree of spatial segregation in species occurrences, a useful indicator of plant-plant interactions and niche differentiation at the community level (Gotelli 2000).

Before assessing the models, multi-collinearity was checked using a generalized variance inflation factors (Fox 2015). In all cases they were below 2, suggesting the absence of collinearity (Chatterjee & Hadi 2001). We select the best model based upon Akaike's information criterion corrected for small samples (AICc). Models with a difference in AICc ($\Delta AICc$) < 2 were considered to be indistinguishable (Burnham & Anderson 2002) and an average explicatory model was estimated. We calculated Akaike weights (w_i) to evaluate the importance of each predictor (Burnham & Anderson 2002), and its relative importance (w_+) was assessed by summing of w_i values of each candidate model in which the predictor appeared.

Functional and phylogenetic analyses were conducted with the R package *Picante*, the linear models and the linear mixed models with R package *lme4* and model selection and calculation of the coefficient of determination with package *MuMIn*.

Results

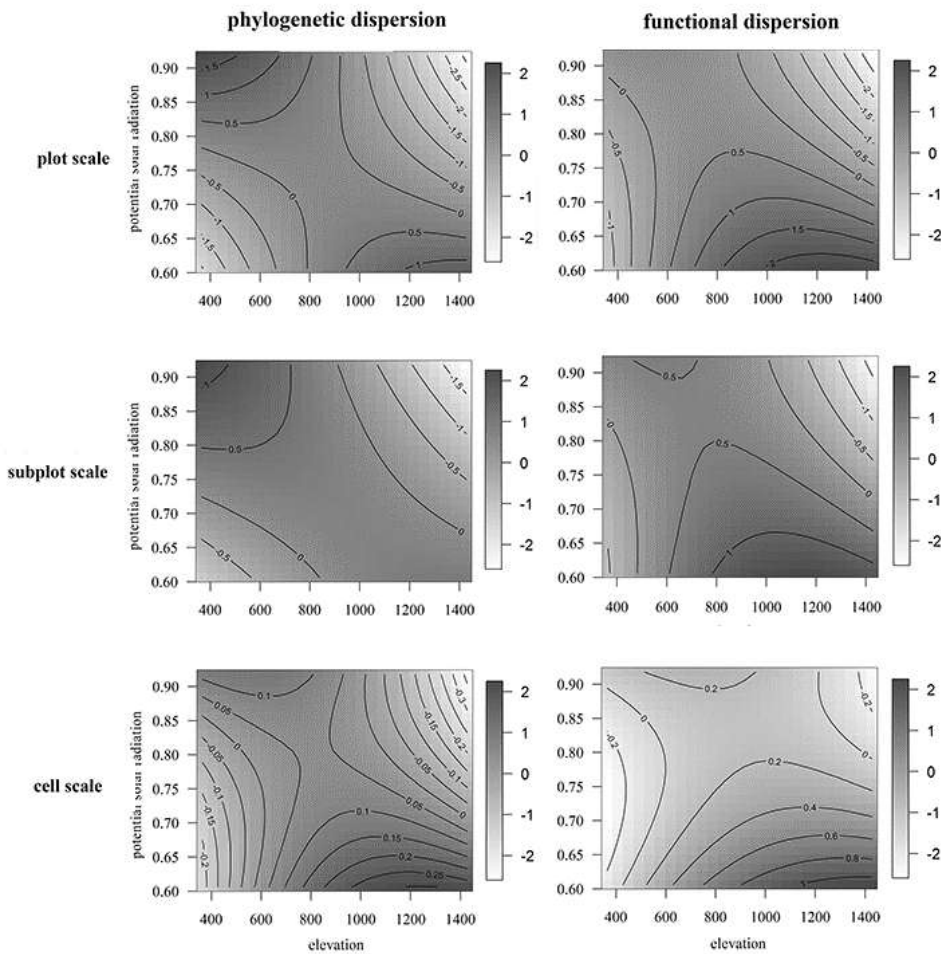
We sampled 100 subplots, distributed in 45 (Maule), 25 (Morado) and 30 (Farellones) subplots. We register 70, 43 and 50 species in the three massifs, respectively, and 105 species in total. The number of species per plot ranged from 12 to 33 with a mean value of 20.8; for subplot those figures ranged from 3 to 22 with a mean value of 11.2; and for cell, they ranged from 3 to 22 with a mean value of 5.5. The most abundant species in the Maule were graminoids as *Festuca acanthophylla* E. Desv. and *Poa denudata* Steud. In the other two massifs, graminoids as *Rytidosperma pictum* (Nees & Meyen) Nicora and *Poa denudata* together with cushion-like shrubs such as *Azorella madreporica* Clos and *Laretia acualis* (Cav.) Gillies & Hook. dominated the alpine vegetation.

Functional dispersion

The functional MPDs were highly variable among communities and relatively constant across scales, averaging 2.02 per plot (range = 0.47 - 3.21), 2.11 per subplot range = 0.10 - 3.60), and 1.43 per cell (range = 0.01 - 3.68). Functional dispersion in the community was significantly influenced by the abiotic factors at any spatial scale (Table 2). In general, the predictor variables with the highest relative importance (w_+) were elevation, potential solar radiation and their interaction (Appendix S4). In particular, the increase in elevation produced a shift from relatively low dispersion values suggesting trait clustering to larger values suggesting overdispersion (Fig. 1). There was also a general increment in overdispersion with increasing potential solar radiation (Fig. 1). Furthermore, the interaction between these two variables produced clustering when there

was a simultaneous increase in elevation and potential solar radiation (Fig. 1). The effect of these two variables was consistent across the different spatial scales (Table 2). At subplot scale, functional trait overdispersion also occurred when aggregated spatial patterns of species predominated (i.e. higher C-score values) suggesting an aggregation of functionally dissimilar species, and clustering when species tend to segregate (Appendix S5).

Figure 1. Predicted relationship of the functional (left) and phylogenetic dispersion (right) with the interaction of potential solar radiation and elevation across plot, subplot and cell scales (from top to bottom). The tone scale on the right of each map indicates the dispersion values. Values > 0 indicate overdispersion. Values < 0 indicate clustering. The black lines represent isoclines.



A significant relationship between the soil fertility index and the functional dispersion was also found (Table 2) but at the finest scale. An overdispersed pattern in higher fertility levels

(i.e. more fertile soil) and a clustered pattern in lower levels of fertility at cell scale was observed (Appendix S5).

Table 2. Model-averaged estimates of model selection and multimodel inference for functional and phylogenetic dispersions.

<i>Dispersion/</i>	plot	subplot	cell
Predictor variable			
<i>Functional dispersion</i>			
elevation	0.020	0.011	0.003
potential solar radiation	23.280	10.687	2.714
elevation X solar radiation	-0.027	-0.014	-0.003
c-score	-	-0.010	-
soil fertility	-	-	0.005
<i>Phylogenetic dispersion</i>			
elevation	0.020	0.012	0.005
potential solar radiation	13.93	8.306	3.396
elevation X solar radiation	-0.022	-0.014	-0.005
c-score	-	-0.004	-0.002
soil fertility	-	-	0.005

Phylogenetic dispersion

The average phylogenetic MPDs were 0.23 per plot (range = 0.06 - 0.32), 0.22 per subplot (range = 0.12 - 0.35), and 0.15 per cell (range = 0.0003 - 0.34). We found similar relationships between the abiotic gradients and phylogenetic dispersion to those of the functional dispersion analyses. In particular, the interaction between elevation and potential solar radiation explained most of the variability of the models at the three spatial scales considered (Table 2; Fig. 1). Regarding soil fertility and C-score index effects, we observed the same trends that were observed for functional dispersion.

Phylogenetic signal of functional traits

The Blomberg's K statistic was lower than 0.002 for all the functional trait measured, indicating phylogenetic signals lower than that expected from a Brownian motion model of trait evolution. However, Pagel's λ indicated rather low phylogenetic signals in all traits except for leaf area where no signal was found (LA: $\lambda=0.69$, $P>0.05$). (SI: $\lambda=0.84$, $P<0.001$; MPH: $\lambda=0.24$, $P<0.01$; SLA: $\lambda=0.56$, $P<0.05$; LDMC: $\lambda=0.66$, $P<0.001$; LT: $\lambda=0.59$, $P<0.05$). The low phylogenetic signals found corresponded to the Spearman correlation between phylogenetic and

functional trait dispersion matrices (0.69, 0.65 and 0.67 (P-values < 0,001) at plot, subplot and cell scales respectively).

Discussion

Functional and phylogenetic dispersion along interacting abiotic gradients at different spatial scales provides valuable information about the processes underlying community structure and assembly (Kawai & Tokeshi 2007). Moreover, our results reinforce the notion that in order to unveil assembly mechanisms not only different spatial scales need to be considered (Messier et al. 2010; Spasojevic & Suding 2012), but also interacting environmental gradients.

While much effort has been devoted to quantifying the functional similarity of species in communities without reference to the abiotic environment (Kraft et al. 2008; Swenson et al. 2012), the tradition in trait-based ecology of relating functional trait means to environmental gradients has naturally lead to the study of functional dispersion along these same gradients (Schöb et al. 2013; Dainese et al. 2015). Although studies focused on one main gradient such as elevation (Read et al. 2014; Pescador et al. 2015), potential solar radiation (Ackerly et al. 2002) or soil nutrient availability (Yang et al. 2014) are useful because they allow a closer investigation into the abiotic mechanisms shaping community diversity and assembly, studies evaluating several gradients at the same time (de Bello et al. 2013; Liu et al. 2013; Xu et al. 2017), including their interaction, are particularly important because communities may be structured in relation to the total environment they experience and not just to a single gradient.

Functional dispersion (i.e. SES of the mean pairwise distance) was influenced by potential solar radiation, a surrogate of energy input that strongly affect important processes (e.g. snowmelt, soil water content, etc.) with critical consequences for plant performance including phenology, plant water content and photosynthesis (Holland & Steyn 1975; Cornwell & Ackerly 2009). This effect differed along elevation as noted by the significant interaction between these two factors (Fig. 1). Functional trait dispersion showed relatively high values suggesting overdispersion in two different environmental scenarios: first when high elevations coincide with low potential solar radiation (i.e. a cold environment) and second, at low elevations but with high potential solar radiation (a rather hot and dry environment) (Fig. 1). These abiotic combinations results in probably the most stressful conditions that can be found in our study sites (see Ackerly et al. 2002; Cavieres et al. 2007; Giménez-Benavides et al. 2007). It is well known that temperature decreases with elevation with freezing temperatures affecting the diversity in higher elevations (Körner 2007). Moreover, in Mediterranean mountains, the short period of vegetative

activity is conditioned simultaneously by the strong summer drought typical of this climate shortening the vegetative growth period. This occurs in opposition to the cold stress gradient of mountains, exacerbating harsh conditions at low elevations (Giménez-Benavides et al. 2007; Körner 2007; Mihoč et al. 2016). Therefore, high potential solar radiation would aggravate drought stress in the lower elevations areas, while low potential solar radiation add environmental harshness to the low temperatures at higher elevations.

The current paradigm suggests that stressful conditions should induce clustered functional diversity patterns due to filtering processes (Cavender-Bares et al. 2006; de Bello et al. 2009), but this is not the case in our Mediterranean climate-type mountains. This could be caused by the incidence of biotic interactions (Pausas & Verdú 2010). Many studies have shown the high importance of biotic interactions as drivers of community assembly (Butterfield & Callaway 2013), also in alpine systems (Mitchell et al. 2009; Schöb et al. 2013; Anthelme et al. 2014). Both positive (i.e. facilitation) and negative (i.e. competition) interactions can generate overdispersion patterns (Soliveres et al. 2012; Gross et al. 2013; Pistón et al. 2015). Overall, facilitation tends to dominate interactions when environmental harshness increases (Callaway et al. 2002; Butterfield & Callaway 2013), whereas when conditions tend to be milder, competition generally increases its importance (MacArthur & Levins 1967; Michalet et al. 2006). Although in alpine habitats a gradient from facilitation dominance in high elevations to competition in the more benign low elevations seems to be the norm (Callaway et al. 2002) a humped-back pattern with maximum stress at the two edges of the gradient (i.e. coldness at the top and summer drought at the low) seems to be typical in Mediterranean mountains (Giménez-Benavides et al. 2007; Pescador et al. 2015) including the Mediterranean Andes (Cavieres et al. 2006). Interestingly, species spatial aggregation (lower C-scores) was related with functional and phylogenetic overdispersion, while species segregation (higher C-scores) generated functional clustering (Table 2). This result suggests the prevalence of facilitation in the local assembly (Götzenberger et al. 2012) because nurses and facilitated plants having divergent trait values are phylogenetically distant, as it has been also shown in other studies including alpine sites (Butterfield et al. 2013; Pistón et al. 2015). Thus, the low functional diversity and convergence where environmental conditions are milder suggest that competition may be the underlying process responsible for this pattern. Although plant-trait based and community assembly literatures have usually suggested that competition drives functional and/or phylogenetic overdispersion (Cavender-Bares et al. 2004), functional and phylogenetic convergence may also be the result of processes such as competitive dominance of some few more competitive species (Mayfield & Levine 2010; HilleRisLambers et al. 2012; Kunstler et al. 2012).

Our findings also suggest that soil fertility may be particularly important in determining the functional structure but only at the finest spatial scale. Soil fertility operated as an abiotic determinant increasing functional clustering when soil fertility was lower (limitation of primary productivity). By contrast, when soil fertility was high, an overdispersion pattern emerged (Table 2). These findings suggest community assembly is mediated by limiting similarity that repulses functionally similar species (MacArthur & Levins 1967), therefore, niche differentiation is required to avoid competition exclusion (Aarssen 1983). Similar results have previously been found in other plant communities when functional diversity is related with different ecosystem functions. For example, Laliberté *et al.* (2013) found increased functional diversity with higher levels of productivity and decreased with low levels in semi-arid grasslands and Mason *et al.* (2012) found divergence and convergence at high and low fertility respectively in rain forest communities.

When the results of phylogenetic dispersion were evaluated, the patterns of the effect between potential solar radiation and elevation, together with the effect the C-score index and the soil fertility were similar to those of the functional dispersion, and consistently at all scales (Table 2). The analysis of phylogenetic signal using Blomberg's K statistic revealed no signal for the plant functional traits studied whereas Pagel's λ indicated a phylogenetic signal present in all traits (except for leaf area), but of low intensity. Under the current theoretical framework if both functional and phylogenetic dispersions are similar, functional trait patterns would show a strong phylogenetic signal (Kraft *et al.* 2007; Cadotte *et al.* 2013; Gerhold *et al.* 2015; de Bello *et al.* 2017). However, this does not need to be the case because unmeasured traits with stronger phylogenetic signal that are low correlated with traits of interest may similarly respond to the gradients. This finding reinforces the idea that the phylogenetic information is complementary to the functional information (Swenson & Enquist 2009) rather than being redundant information or a proxy of the functional structure (Mason & Pavoine 2013; Pavoine *et al.* 2013). Our results also suggest that the strength of local assembly processes remains strongly connected with spatial scales (Chalmandrier *et al.* 2017). Thus, functional trait and phylogenetic dispersion were coupled consistently across spatial scales. Many studies have showed that discrepancies with different patterns of dispersion, functional or phylogenetic, occur among different spatial scales (Cavender-Bares *et al.* 2006; Swenson *et al.* 2007; Yang *et al.* 2014). In our case, probably due to the sharp shifts in environmental abiotic conditions along a long elevational gradient, the dispersion patterns remain similar and tight across scales.

Taken together our results suggest the dominance of abiotic gradients interactions in the functional and phylogenetic dispersion structure although they also reinforce the general idea that

biotic interactions and other very fine local factors such as soil fertility heterogeneity are simultaneously operating.

Conclusions

Our results indicate the importance of evaluating more than one abiotic gradient at a time. Interactions (additive or synergistic) between gradients are expected to be common and analyzing these interactions can give novel perspectives to the community assembly processes. Our study demonstrates how these interactions may act. Stress in these mountains is very intense at both ends of the elevational gradient due to the existence of opposite temperature and moisture stress gradients (Mihoč et al. 2016). Solar radiation must be taken into account since it can attenuate or exacerbate environmental harshness associated to elevation. This interaction between both factors produced functional and phylogenetic overdispersed patterns resulting from facilitative interactions where the conditions are more stressful. On the contrary, where the conditions are milder, dominance of a few species that are more competitive could lead to clustered patterns. Thus, our results support the hypothesis that biotic interactions modulated by environmental conditions are important for alpine plant community assembly. These patterns were consistent across spatial scales. Finally, it is worth to note that the functional and phylogenetic patterns and drivers run in parallel despite the fact that the considered functional traits had no phylogenetic signal. This suggest that first, the two diversities are not redundant (Swenson & Enquist 2009), and second, the extreme abiotic conditions these communities face produce convergence in the patterns and mechanisms of these two complementary diversities.

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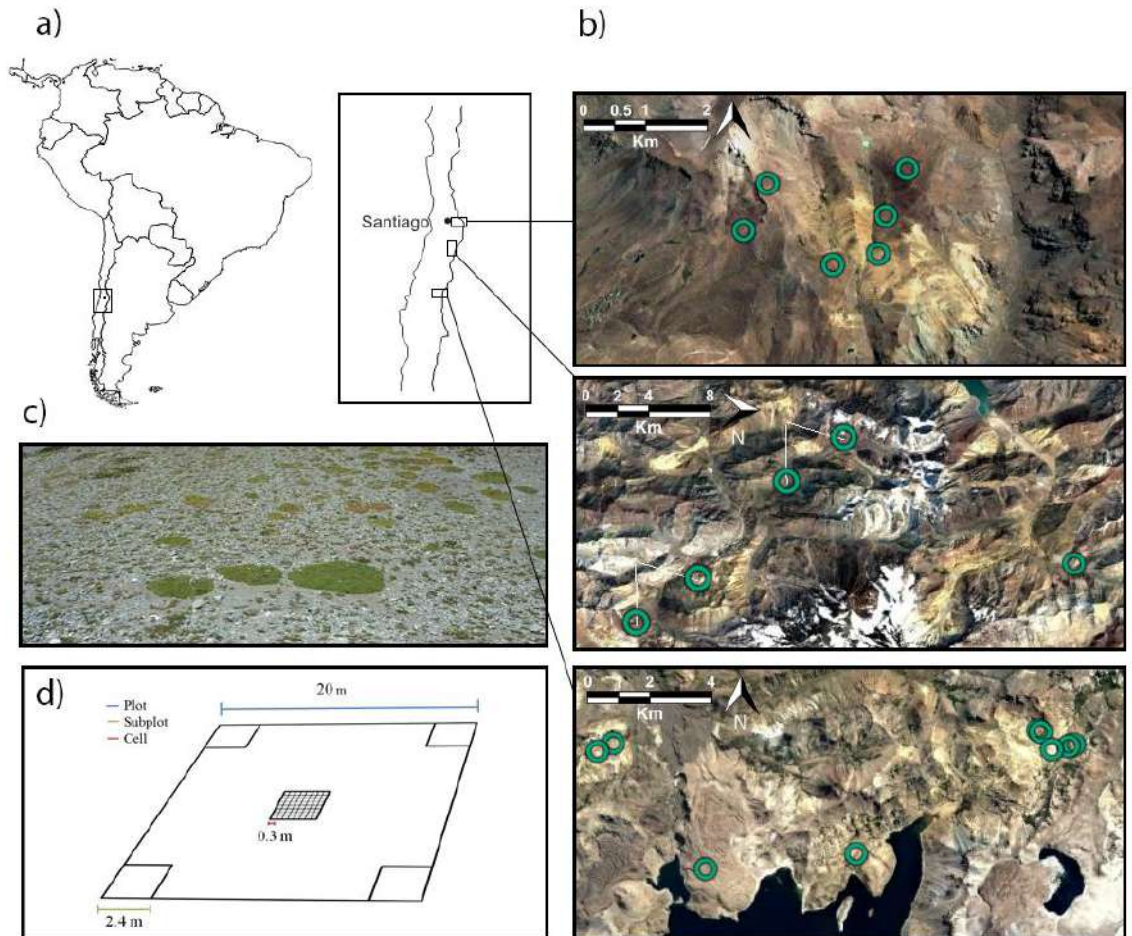
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Appendices

Appendix S1. Schematic of experimental design. **a)** Localization of study areas in the central Chilean Andes; **b)** plot distribution in each zone; **c)** typical structure of vegetation; and **d)** sampling design structured across three scales.



Appendix S2. Methods of estimation of soil properties.

Soil organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulphuric acid (Yeomans & Bremner 1988). Total N and available P was determined on a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in the Nutrilab/URJC lab after digestion with sulphuric acid and Kjeldahl's catalyst (Anderson & Ingram 1994). Potassium (K) was measured with the same analyzer after the soil samples had been shaken with distilled water (1:5 ratio) for 1 h. Enzymatic activities were estimated using the methodology described in Eivazi & Tabatabai (1988; β -glucosidase) and Tabatabai and Bremner (1969; acid phosphatase).

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Yeomans, J.C., & Bremner, J.M. 1988. A rapid and precise method for routine determination of organic carbon in soil. *Communications in Soil Science and Plant Analysis* 19: 1467–1476.

Appendix S3. Phylogenetic analysis

In the first instance, available species sequences from GenBank were downloaded (45 sequences). The rest of the species sequences (165 sequences) were obtained in the laboratory. Specifically, 20 mg of fresh leaf was collected from three individuals per species. The samples were then disrupted and homogenized with a TissueLyser LT (Qiagen, Valencia, CA, USA) using glass beads after storing and drying in silica-gel for one month. Total DNA was extracted with DNeasy Plant Mini-Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions.

The *rbcL* barcode was amplified in a 25 μ L reaction with 2 μ L of DNA in 23 μ L mix-reaction - 2.5 μ L of Ta buffer 2 mM with $MgCl_2$, 1 μ L of dNTP Mix (0.4 mM), 1.25 μ L of reverse and forward primer and 1.25 U Taq DNA Polymerase (Biotools, Madrid, Spain)-. The *matK* barcode was amplified by puReTaq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Uppsala, Sweden). PCR amplification was performed on a S1000 Thermal Cycler (Bio-Rad, Hercules, CA, USA). Primers for PCR, sequencing and PCR cycling conditions used in this study are provided in Appendix S4. Other primer pairs were necessary for samples that either failed in PCR amplification (see Appendix S4). Amplified PCR products were purified using the ExoSap purification kit® (USB Corporation, Cleveland, OH, USA). The samples were sequenced by MACROGEN (Seoul, Korea and Amsterdam, Netherlands). In order to corroborate the species identity two individuals were used to obtain the forward and reverse strands. Consensus sequences were assembled using Sequencher 4.1.4 software (Gene Codes Corporation, Ann Arbor, MI, USA) and aligned with MAFFT online v. 7, then checked manually with Mesquite version 2.6. Phylogenetic analyses were conducted with the R package *phangorn* (Schliep 2011) using the maximum likelihood model with 100 bootstrap replications. To obtain phylogenetic tree we used a species pool composed by the species of this study together with similar ecosystem species from South of Chile and Spain. In total, we used 573 DNA sequences of which 105 appeared in our sample area.

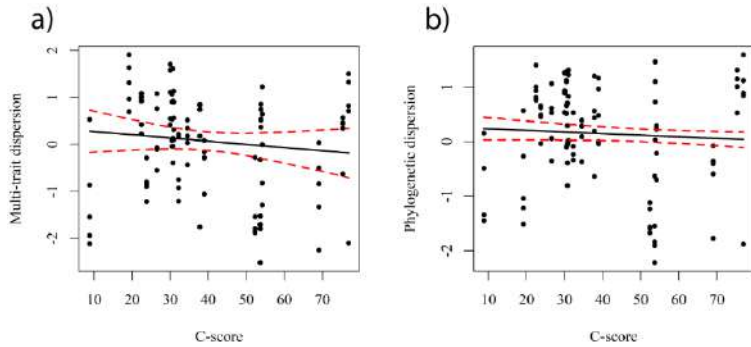
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Appendix S4. Results of model selection and multimodel inference for functional and phylogenetic dispersion at three studied scales. We detailed the $\Delta AIC_c < 2$ set of models. X indicates variable inclusion in each individual model. wi: Akaike weights. w+: relative importance of each predictor for each averaged model. PSR: Potential solar radiation

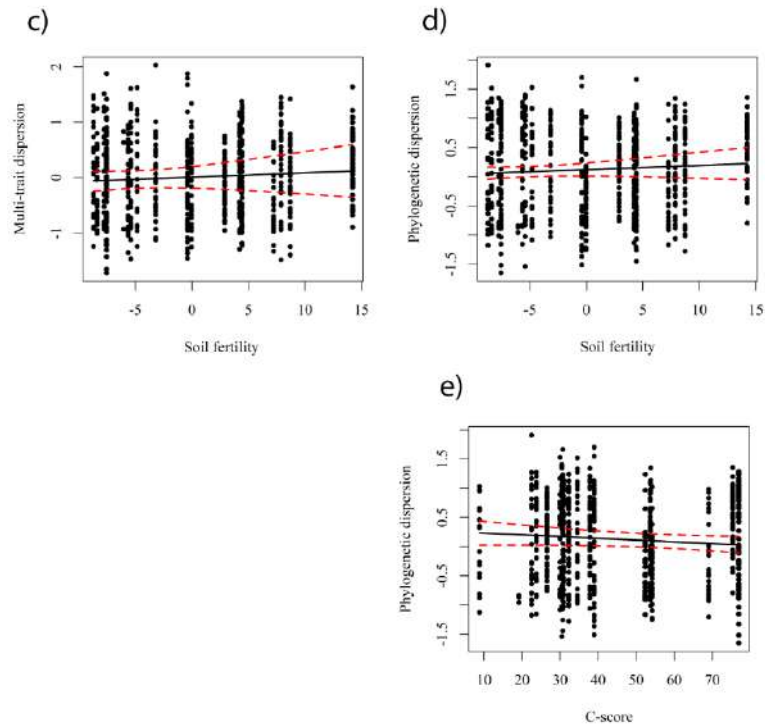
Dispersion/ Scale/ Models	elevation	PSR	elevation X PSR	C- score	Fertility	AICc	ΔAIC_c	wi
Functional dispersion								
plot								
1	X	X	X			63.8	0	1
w+	1	1	1	-	-			
subplot								
1	X	X	X	X		244.5	0	0.703
2	X	X	X			245.6	1.13	0.297
w+	1	1	1	0.63	-			
cell								
1	X	X	X		X	1432.9	0	0.53
2						1434.2	1.21	0.257
3	X	X	X			1434.5	1.58	0.213
w+	0.78	0.78	0.78	-	0.4			
Phylogenetic dispersion								
plot								
1	X	X	X			60	0	1
w+	1	1	1	-	-			
subplot								
1	X	X	X			220.9	0	0.543
2	X	X	X	X		221	0.04	0.457
w+	1	1	1	0.49	-			
cell								
1	X	X	X			1463	0	0.4
2	X	X	X	X		1463.8	0.79	0.273
3	X	X	X		X	1464.7	1.69	0.167
4	X	X	X	X	X	1464.8	1.75	0.159
w+	1	1	1	0.43	0.33			

Appendix S5: Relationships between the functional dispersion (left) and phylogenetic dispersion (right), with C-score index (a, b and e) and soil fertility (c and d) for the GLMM models. The fitted lines indicate results from GLMMs with confidence intervals.

subplot scale



cell scale



Chapter 3

**Biotic interactions at the extremes of abiotic gradients
shape the functional structure of an alpine plant
community: null models reproduce assembly rules**



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Arantzazu L. Luzuriaga & Adrián Escudero**

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Abstract

1. Ongoing challenges in community ecology involve understanding plant assemblies and their underlying deterministic mechanisms. In order to determine the prevalence of abiotic and biotic assembly processes along environmental gradients (i.e., elevation, solar radiation, and soil fertility), we evaluated the discrepancies between the observed and expected functional diversity under three realistic null models, where each could reproduce the assembly under the action of different ecological rules (biotic, abiotic, and a mix of both).

2. We fitted the occurrence probabilities of species using (1) binomial GLMs based on environmental predictors, (2) Beals smoothing based on the species co-occurrence patterns, and (3) binomial GLMs based on both environmental covariates and latent variables describing the correlations between species for the (1) abiotic, (2) biotic, and (3) mixed abiotic–biotic null models. We surveyed the grasslands above the timberline in the central Pyrenees.

3. Our null models could reproduce the observed functional structures but their performance differed, where the abiotic models had the worst performance. Furthermore, using the abiotic null models, we found discrepancies between the expected and observed values (i.e., large standardized effect sizes as estimates of functional discrepancy) at the extremes of the environmental gradients (i.e., altitude and solar radiation). In particular, we found functional divergence in the maximum plant height, leaf thickness, and multi-trait combination at higher elevations and functional convergence in the seed mass and maximum plant height with increasing solar radiation, thereby suggesting the limited performance of these abiotic models and the important roles of biotic interactions.

4. We found functional divergence in maximum plant height, leaf thickness, and the multi-trait combination at higher elevations, and convergence in seed mass and maximum plant height with increasing solar radiation.

5. *Synthesis.* Generating realistic null assemblages under the action of particular assembly rules allowed us to disentangle the roles of biotic and abiotic rules in the assembly of these rich grasslands. We conclude that both deterministic mechanisms are operating simultaneously, with foreseeable shifts at the extremes of the environmental gradients, where facilitation in the most stressful environments and competition in the most benign environments may become prevalent.

Keywords: Alpine ecosystem; Assembly rule; Community assembly; Ecological gradient; Functional trait; Null model; Species interaction

Introduction

Understanding plant community assemblies and the underlying mechanisms of species co-existence are ongoing challenges in community ecology (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Lortie et al., 2004; Weiher & Keddy, 1995). The plant species composition of a natural assemblage is the net result of stochastic and deterministic processes that act simultaneously (Escudero & Valladares, 2016; Vellend et al., 2014). A consensus exists that the limitations imposed by the abiotic environment together with plant–plant interactions are critical among the deterministic processes, which are sometimes called ecological assembly rules (Götzenberger et al., 2012). Unfortunately, disentangling the effects of abiotic and biotic processes under field conditions remains complicated. However, trait-based ecology (see Shipley et al., 2016) provides a complete toolbox for addressing this dilemma. The idea that all species are ecologically equivalent is not easily defensible (Doncaster, 2009), so a natural next step is to consider their individual roles in the community based on the life-history and ecological traits of each plant species (Diaz, Cabido, & Casanoves, 1998; Keddy, 1992). Under this functional perspective, the plant species that thrive together in a realized assemblage are selected first from the regional species pool by abiotic filters that act at relatively coarse spatial scales according to their functional traits (Lavorel & Garnier, 2002; Mayfield, Boni, & Ackerly, 2009). Second, they outcompete other species that pass through the first filter but with functional traits that give them inferior competitive abilities (Chesson, 2000; MacArthur & Levins, 1967).

One of the most extensively used approaches for disentangling the roles of these two deterministic mechanisms in specific communities is the so-called null modelling approach (see Gotelli & Graves 1996). This powerful approach is based on comparing the distributions of the values of any functional community feature observed in natural assemblages with those expected in randomly assembled communities. Unfortunately, although many null model algorithms (Botta-Dukát & Czúcz, 2016; Götzenberger et al., 2016; Hardy, 2008; Miller, Farine, & Trisos, 2017; Perronne, Munoz, Borgy, Reboud, & Gaba, 2017) and randomization schemes (Chalmandrier et al., 2013; Cornwell, Schilke, & Ackerly, 2006; de Bello et al., 2012; Miller et al., 2017) have been proposed, there is no general consensus regarding the most appropriate algorithms and randomization schemes for addressing specific ecological questions (Ulrich et al., 2017; Ulrich & Gotelli, 2013). Most of the null models used to assess the functional structure of a community are based on the randomization of species occurrences according to one or several well-known matrix rules (Gotelli & Graves, 1996), e.g., maintaining each species frequency (in order to account for ecological differences among species) and/or restricting sample species (in

order to control for differences in soil fertility or other microsite conditions among sites) (Gotelli, 2000; Gotelli & Entsminger, 2003). However, these models have a low capacity for separating specific ecological processes (Gotelli & Ulrich, 2012). Hence, making a good choice among these null models is critical because they can yield very different conclusions (de Bello, 2012).

In order to minimize the limitations of traditional null models based on reshuffling species, more realistic approaches are needed that can reproduce assemblages under explicit assembly processes. In this case, if the observed pattern is not significantly different from that expected, we cannot exclude this process as an ecological deterministic rule. Deviations from these null expectations would imply roles for other unconsidered mechanisms (Gotelli & Ulrich, 2012). For instance, the simplest way of generating environmentally constrained null communities is by randomizing the species composition within sites sharing a common habitat, elevational stratum, or vegetation belt (de Bello, 2012; Hausdorf & Hennig, 2007; Jung, Violle, Mondy, Hoffmann, & Muller, 2010). However, among other problems, this simple approach is affected by the inherent loss of information associated with discretizing environmental gradients, including equalizing the niche breadth for groups of species. To address some of these issues, several studies (e.g., Cornwell & Ackerly, 2009; de Bello et al., 2012) have considered species-centred null models of niche breadth based on the range (i.e., the extremes) of values measured for the relevant environmental variable(s) among the sites where each species has been observed. However, these models assign the same probability of occurrence in a plot to all species with a niche breadth that includes the environmental conditions in the plot, irrespective of whether these conditions are on the limit of the niche breadth or close to the ecological optimum for the species. Furthermore, Peres-Neto et al. (2001) proposed estimating the probabilities of species occurrence as a function of environmental conditions using classification techniques such as linear discriminant analysis or logistic regression. Null models based on this approach can be employed to assemble null communities where the species present would suit the site's abiotic conditions. However, the patterns of functional convergence identified based on any of these “*classical*” null models have generally been attributed to environmental forces but without considering the fact that distribution patterns are responses due to biotic determinants as well as abiotic mechanisms (Cadotte & Tucker, 2017; Kraft et al., 2015). Thus, incorporating biotic constraints in the null models of community assembly could help to disentangle and/or evaluate the relative importance of biotic *versus* abiotic processes in the assembly, and consequently in the functional attributes of the community. However, to the best of our knowledge, no previous studies have attempted to incorporate biotic constraints into null models of community assembly (but see D'Amen, Mod, Gotelli, & Guisan, 2017), although there is strong consensus that considering biotic interactions

will improve the ability of statistical models to predict species occurrences (Anderson, 2017; Godsoe & Harmon, 2012; Kissling et al., 2012). For example, it has been shown that the so-called “community based modelling of species distributions” (Ferrier & Guisan, 2006) can capture meaningful biotic interactions among species and improve the prediction of individual species occurrences (Baselga & Araújo, 2009).

In this study, we tested the systematic use of three types of null models, where each could reproduce the assembly of plant communities under the action of specific ecological rules. In particular, we generated null assemblages in response only to abiotic determinants, to biotic interactions, and to both biotic and abiotic ecological rules. Comparing the functional structures of the observed assemblages with those generated by these three type of null communities (abiotic, biotic, or both) may help to understand the assembly rules involved, as well as providing information regarding the prevalence and deviations of specific assembly processes in the field along environmental gradients.

For the abiotic null model, we fitted binomial generalized linear models (GLMs) based on environmental predictors measured in the field (including climatic and soil covariates) to the presence/absence of each plant species. We assumed that niche differences are important and each species was entered in the null communities as a probabilistic function of the abiotic conditions found in each site (i.e., niche preferences) (Peres-Neto et al., 2001). These null models generated null communities that responded exclusively to the abiotic conditions in each site. For the biotic null models, we fitted the occurrence probabilities of species using Beals smoothing (Beals, 1984; De Cáceres & Legendre, 2008), which estimates the probability of encountering a given species at a site as a function of the species co-occurrences pattern in the observed community. Therefore, this model assembled null communities based mostly on the actual species (i.e., biotic) interactions. In the third type of null models based on the biotic and abiotic constraints, the probability of occurrence was estimated for each species according to the recently proposed joint species distribution model framework (Pollock et al., 2014; Warton et al., 2015), where binomial GLMs of the presence and absence of each species were fitted to both the environmental covariates and latent variables describing the correlations between species (Hui, 2016). Thus, the null communities were generated according to the estimated likelihood of species occupancy at each site, including the responses to the abiotic environment and biotic interactions. In summary, we obtained null communities by considering only the abiotic limitations (niche separation), biotic interactions, or both. Comparing the functional structures of the observed and null communities provided insights into the assembly rules that dominated a specific plant community. Furthermore, evaluating the discrepancies between the expected and

observed functional structures for each ecological rule along abiotic gradients indicated the prevalence of each rule along the gradient.

In this study, we surveyed the alpine vegetation along a large elevational gradient from 1660 to 2530 m in the central Pyrenees. The vegetation exhibited marked zonation and a high turnover rate, which suggested the prevalent effects of deterministic processes on the organization of the realized assemblages (Ninot et al., 2007), thereby allowing us to explore the response of the functional structure of the communities to these assembly rules. We examined the prevalence of these assembly processes with respect to three critical key environmental factors: elevation, soil fertility, and potential solar radiation. We addressed the following specific questions: (1) could the use of environmentally and/or biotically constrained null models combined with the functional trait distribution allow the inference of assembly rules? and (2) what type of mechanism (biotic or abiotic) was responsible for the observed functional structure of the communities?

Methods

Study area

The study was conducted in the alpine grasslands of the Ordesa and Monte Perdido National Park (42°40'18"N 0°03'20"E), which is located in the Spanish Central Pyrenees and their surroundings, including the French Pyrenees. We sampled the grasslands above the local *Pinus uncinata* treeline, including subalpine and alpine vegetation belts, but we avoided rocks, screes, snowbeds and waterlogged habitats.

In the study area, the climate is temperate with a mild influence of the Mediterranean-type climate, which is stronger at lower elevations. The average annual temperature and precipitation values are 4.9°C and 1650 mm, respectively (at 2200 m a.s.l.: AEMET/IM, 2011). Precipitation occurs mainly during the autumn and spring. Snow cover lasts from October to May, although the duration of the snow cover varies widely among zones according to the elevation and orientation. The vegetation mainly comprises limestone rocky pastures dominated by *Festuca gautieri* (Hackel) K. Richt. subsp. *scoparia* (Kerner ex Nyman) Kerguelen, which is accompanied by a wide variety of species such as creeping and cushion chamaephytes (e.g., *Astragalus sempervirens* Lam, *Sideritis hyssopifolia* L., *Androsace villosa* L., or *Thymus* gr. *serpyllum* L.) and other grasses (e.g., *Koeleria vallesiana* (Honck.) Gaudinand *Helictotrichon sedenense* (DC.) Holub). The pasture-like community is always patchy and the total cover of

perennial vegetation varies from 5% to 35% (Ninot et al., 2007). Low intensity cattle grazing occurs during the growing season.

Fieldwork and environmental factors

We conducted the surveys throughout the summer seasons in 2013 and 2014. We sampled 27 sites covering the whole elevational range throughout the territory (from 1650 to 2550 m a.s.l.), where we considered a complete range of aspects and slopes. At each site, we established a 20 m × 20 m plot, which was representative of the surrounding vegetation. In each plot, we placed five 2.4 m × 2.4 m quadrats, with one in each corner and a fifth at the centre, and we recorded the cover values for each plant species within each quadrat. This sample size is adequate for including complete representation in this type of pasture (see Pescador, De Bello, Valladares, & Escudero, 2015). The elevation and aspect were obtained for each plot by using a GPS (Garmin Colorado-300, Garmin Ltd, Olathe, USA) and the slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Aspect and slope values were used to calculate Gandullo's potential solar radiation coefficient (Gandullo, 1974). Two soil cores (5 × 10 cm) were taken within each corner plot, with one in an open area and the other under a vegetated patch. Each soil core was air dried for one month and sieved to 2 mm. We estimated the total organic carbon (C), total nitrogen (N), total phosphorus (P), potassium (K), β -glucosidase, and phosphatase content, as well as the soil pH and electric conductivity (for more details see López-Angulo, Swenson, Cavieres, & Escudero, 2018). The soil fertility estimated based on the multifunctionality index proposed by Maestre et al. (2012) was calculated for all the soil variables as an integrated surrogate of the capacity of each realized assemblage to sustain multiple ecosystem functions (Maestre et al., 2012). Soil variables for the centre quadrat were estimated as the average of the other four quadrats in the plot. We square root-transformed the soil variables and calculated weighted Z-scores for each individual soil variable and position (bare or vegetated areas) by using the mean cover observed for bare ground and vegetated areas in each quadrat as weights. The multifunctionality index was the average of the Z-scores for the eight soil variables assessed.

Trait measurements

During July 2014, several plant functional traits were measured for 96 species, which represented 94% of the accumulated cover in the study area and at least 80% of the plant cover for each quadrat, which was sufficient to represent the functional composition of the local plant communities (Pakeman & Qusted, 2007). For each species, we measured five traits in 10 randomly selected individuals at the site where each species was most abundant. The selected

traits were the plant vegetative maximum height (Hmax), leaf dry matter content (LDMC), specific leaf area (SLA), leaf thickness (LT), and seed mass (SM). According to the leaf-height-seed plant ecology strategy scheme proposed by Westoby (1998), these five traits reflect key the ecological strategies for plants. The traits were measured according to the protocols outlined by Cornelissen et al. (2003). Rarely, some traits were impossible to measure in the field. Thus, we completed our trait database with information from the Royal Botanic Gardens Kew Seed Information Database (Flynn, Turner, & Stuppy, 2008) and from the LEDA traits database (Kleyer et al., 2008) (0.3% of entries and 0.02% of the cumulated cover for the whole community). Trait data from some species (0.08% of entries and 0.1% of the accumulated cover for the whole community) were inferred from congeneric information in the aforementioned databases.

Functional diversity

Traits were log-transformed as necessary to ensure normality. In order to estimate the functional distances among species, we computed the Gower distance between their mean trait values for each single trait and for the ensemble of traits (i.e., “multi-trait”) using the *gowdis* function in the *FD* package for R v 3.3.3 (R Core Team, 2016). To estimate the functional diversity (for each trait and for all traits together) in each community, we computed the weighted mean pairwise distance (MPD) (i.e., weighted by the relative cover of each species in each community). MPD was computed using the *mpd* function in the *picante* package (Kembel et al., 2010). This index is independent of the number of species and it is highly correlated with other widely used indices of functional diversity (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). MPD was also calculated for each null assemblage generated.

Null models of community assembly

We used a modelling framework that reflected the metapopulation dynamics of the system because we expected species growth to depend on the environmental conditions, but the presence and absence of species in communities should be determined by stochastic and deterministic processes. This framework comprises three main steps: 1) fitting different models of occurrence (i.e., probability of occurrence) in each plot for each species; 2) fitting statistical models of abundance in each plot (i.e., cover) for each species; and 3) building null communities by combining the predictions from models 1 and 2.

Models of species abundance. First, we performed principal component analysis (PCA) based on 11 environmental variables (the eight soil variables plus elevation, slope, and potential solar radiation) using the *princomp* function in the *stats* package. We then fitted linear models

(with Gaussian errors) to the species abundances (i.e., cover) using the first five PCA axes, their quadratic terms, and all the interaction terms as explanatory variables. Standard model checking showed that these models were acceptable, and thus transformation was not needed. In addition, model checking found no problematic patterns. A stepwise variable-selection procedure based on Akaike's information criterion (AIC) was used to find the best predictive model for each species. Linear models and stepwise selection were performed with the *glm* function in the *stats* package and *stepAIC* in the *MASS* package in R (R Core Team, 2016).

Models of species occurrence. We employed three different strategies to model species occurrence: abiotic, biotic, and mixed abiotic–biotic.

For the so-called abiotic null model, we modelled the species distribution according to only the abiotic environmental variables. We fitted GLMs (with a binomial error distribution and using a logit link function) to the species occurrence data (i.e., presence/absence) using the first five PCA axes, their quadratic terms, and all the interaction terms as explanatory variables. A stepwise variable-selection procedure based on AIC was used to find the best predictive model for each species.

We used Beals smoothing to fit the biotic models (Beals, 1984; De Cáceres & Legendre, 2008), which estimates the probability of occurrence for target species in a quadrat according to the observed species composition and the pattern of species co-occurrence for the target species with other species in the whole community. Thus, the probability that a given target species j occurs in a quadrat i is defined as:

$$p_{ij} = (1/S_i) \sum_{k=1}^s \frac{m_{jk}x_{ik}}{n_k}, \quad \text{eqn 1}$$

where S_i is the number of species in quadrat i , m_{jk} is the number of joint occurrences of species j and k , n_k is the number of occurrences of species k in the community matrix, x_{ik} is the incidence (0 or 1) of species k in quadrat i , and s is the number of different species in the community (De Cáceres & Legendre, 2008). Beals smoothing was performed with the *beals* function in the *vegan* package (Oksanen et al., 2013).

Finally, we fitted mixed abiotic–biotic models where we simultaneously modelled species occurrence according to the abiotic environment and the pattern of species co-occurrence using latent variable models (LVMs) (Bartholomew, Knott, & Moustaki, 2011; LVM; Skrondal & Rabe-Hesketh, 2004). A LVM is a function (similar to a GLM) fitted to both observed and non-observed (i.e., latent variables) predictors. The latent variables account for any residual

covariance not explained by the environmental conditions, including the residual correlations between species (Warton et al., 2015).

One possible way of defining a LVM for binomial data is:

$$\text{probit}(p_{ij}) = \alpha_i + \beta_{0j} + \mathbf{x}'_i \boldsymbol{\beta}_j + u_{ij}, \quad \text{eqn 2}$$

where p_{ij} is the probability of finding species j in sample i , β_{0j} is an intercept, $\boldsymbol{\beta}_j$ is a vector of regression coefficients, \mathbf{x}'_i is the transposed vector of environmental predictors measured in sample i , and u_{ij} is a random effect defined as a function of latent variables \mathbf{z}_i and factor loadings $\boldsymbol{\lambda}_j$, i.e., as $u_{ij} = \mathbf{z}'_i \boldsymbol{\lambda}_j$ (Warton et al. 2015). Latent variables have been considered as quantities that mediate interactions between taxa (i.e., “interaction occurrences”) (D’Amen et al., 2017; Kissling et al., 2012). We fitted LVMs to the species incidence data (i.e., as binomial response) based on the five PCAs, their quadratic terms (as observed predictors), and two latent variables using probit as the link function. These analyses were implemented with the *boral* function in the *boral* package (Hui, 2016).

Building null communities. For each of our null model strategies (i.e., abiotic, biotic, and mixed abiotic–biotic), we combined predictions from the respective fitted species occurrence model and the fitted species abundance model within a bootstrap framework. In particular, for each simulated assemblage, we used the probabilities of each species occurring in each quadrat to simulate 999 null assemblages per quadrat and per null model with the identical number of species in each quadrat relative to those found in the observed assemblages.

Statistical analyses

For each of the 135 quadrats, we calculated the standardized effect size (SES: Gotelli & McCabe, 2002) of the functional diversity (i.e., $SES = (MPD_{obs} - \overline{MPD}_{sim}) / sd(MPD_{sim})$) for each functional trait independently and for all the traits together (“multi-trait FD”).

We fitted linear mixed models (Pinheiro & Bates, 2000) based on elevation, potential solar radiation, and soil fertility to evaluate whether the relative strengths of abiotic or biotic mechanisms related to the community functional structure (i.e., discrepancies between the observed and expected functional diversities estimated as the SES values) varied along stress gradients. We also included the quadratic term of elevation as a fixed effect and considered the plot as a random effect. We tested for collinearity between the different environmental predictors using the variance inflation factor before building the models, where the values were below 2 in all cases, thereby suggesting the absence of collinearity (Chatterjee & Hadi, 2001). The normality

of the standardized residuals was visually checked for all of the models. We estimated the statistical significance of each predictor using type-II analysis of variance.

Results

We registered 159 species in the 135 sampled quadrats (27 plots). The species richness per quadrat varied from 4–42 with a mean value of 18.8. In addition to *Festuca gautieri* subsp. *scoparia* (A. Kern. & Hack.) Kerguélen, the most abundant species were other graminoids such as *Koeleria vallesiana* (Honck.) Gaudin subsp. *vallesiana* and *Helictotrichon sedenense* (DC.) Holub, as well as some creeping chamaephytes, including *Thymus* gr. *serpyllum* L. and *Galium pyrenaicum* Gouan. The latter species had similar incidence frequencies (number of occurrences) to graminoids but their cover levels were always lower. About half of the recorded species occurred in less than 5% of the quadrats (less than six occurrences). The remaining species occurred in at least 20% of the quadrats (135), where the maximum occurrence rate for one species was 115 (89%) for *Thymus* gr. *serpyllum* L.

Our three models reproduced the observed functional structures with a very low number of significant deviations (i.e., differences between expected and observed functional patterns). Overall, the observed functional diversity was not significantly different from that expected, irrespective of the trait analyzed and the null model employed (Table 1). The percentage of observed quadrats where the observed functional diversity differed significantly from the expected functional diversity varied from 0% to 6.66%. More deviant quadrats were found for SLA under the abiotic null model.

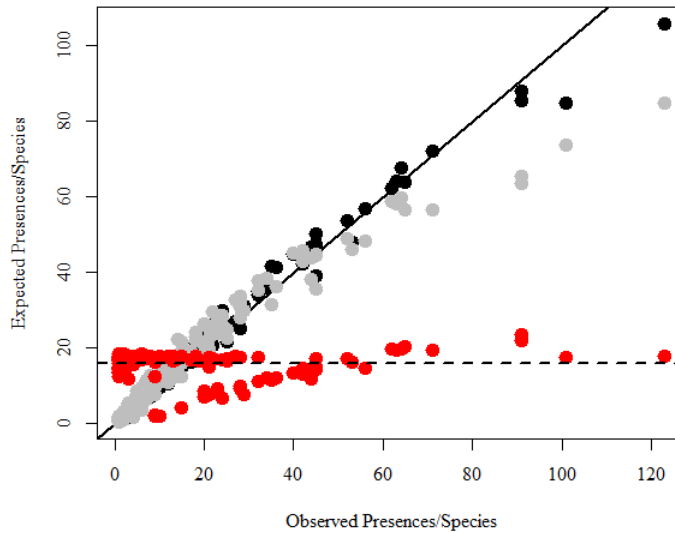
Table 1. Numbers of quadrats where the observed functional diversity differed significantly from the expected functional diversity under the null models ($-1.96 < \text{SES} < 1.96$) among 135 quadrats.

Null model	Trait					
	SM	SLA	LDMC	LT	Hmax	Multi-trait
Abiotic	0	9	0	2	0	0
Biotic	0	4	4	1	1	4
Mixed	1	2	4	6	3	4

We found differences among the null models in terms of their ability to reproduce some functional properties of the studied assemblages. For instance, the biotic and mixed null models reproduced the frequency of appearance for each species fairly well (Fig. 1). By contrast, the

expected frequencies of the less abundant species under the abiotic null model were mostly similar to the expected frequency if they had entered the null communities randomly (i.e., with a frequency equal to the ratio between the total incidence and the total number of species; Fig. 1, Appendix 1). For only some species, there was a linear relationship between the expected and observed frequencies for the abiotic null models, but the expected frequency was always lower than the observed frequency.

Figure 1. Relationship between the observed frequency of each species and the expected frequency (average of 999 randomizations) estimated under the abiotic null model (red points), biotic null model (gray points), and mixed abiotic–biotic null model (black points) in the total sample. The dotted line represents the expected value if all species enter randomly (the ratio between total incidence and the number of species, i.e., ~16 occurrences).



The discrepancies between the observed and expected functional diversity estimated as the SES values (referred to as the functional discrepancy (FDisc) in the following) for all the functional traits (including the multi-trait combination) were related to some environmental predictors (Table 1). In particular, for the abiotic null assemblages, we found a significant positive effect of elevation (i.e., FDisc tended to be larger than expected as the elevation increased) on all traits (including the multi-trait combination), a significant positive effect of the squared term of elevation on the discrepancies for LT, and a significant negative effect of potential solar radiation on the FDisc in the maximum plant height. For the biotic null models, we only found a significant effect positive of elevation on the FDisc in the maximum plant

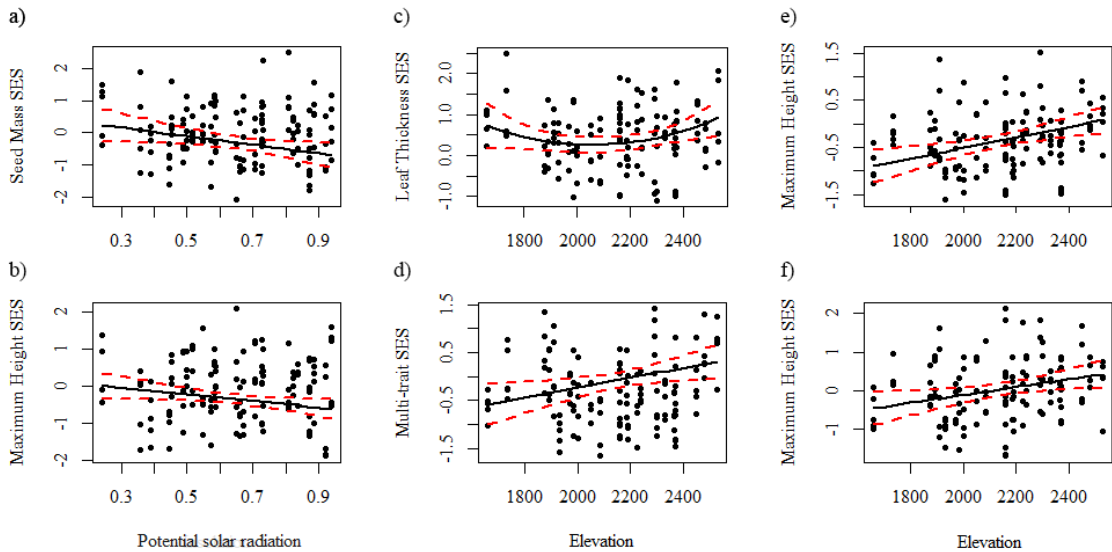
height. By contrast, none of the environmental predictors had significant effects on any of the discrepancies estimated from the mixed abiotic–biotic null models (Table 2, Fig. 2). Finally, we found no significant effect of soil fertility on the functional structure, and the FDisc in SLA and LDMC were not influenced by any abiotic factors.

Table 2. Coefficients of the linear mixed effect models for examining the effects of environmental variables on the SES of the functional diversity (discrepancies between observed and expected values) for each null model considered. Only results for models with significant effects are shown.

	Abiotic model	Biotic model	Mixed abiotic– biotic model
Seed mass			
Intercept	−0.31		
PSR	−0.25		
Elevation	0.19 *		
Soil fertility	0.1		
Maximum plant height			
Intercept	−0.353	0.04	
PSR	−0.168 **	−0.12	
Elevation	0.251 *	0.23 *	
Soil fertility	0.098	0.02	
Leaf Thickness			
Intercept	0.282		
PSR	−0.109		
Elevation ²	0.148 *		
Elevation	0.114 *		
Soil fertility	0.084		
Multi-trait			
Intercept	−0.083		
PSR	−0.158		
Elevation	0.228 *		
Soil fertility	0.063		

Figure 2. Significant relationships between the SES values of the functional diversity (discrepancies between observed and expected functional diversity) with the potential solar radiation and elevation

gradient. Only significant relationships are shown. The fitted lines indicate the results obtained by the linear mixed effect models with confidence intervals. Results in (a) to (e) were obtained under the abiotic null model, and in (f) under the biotic null model. No significant models were found for the mixed models.



Discussion

In this study, comparisons between the functional structures of observed assemblages and the functional structures expected under the effects of abiotic, biotic, or both assembly rules allowed us to infer whether these two critical ecological mechanisms individually or simultaneously determine the community assembly, as well as their relative prevalence along environmental gradients. Our three realistic null models could reproduce the functional diversity structure for the multi-trait combination and for all the individual plant traits, but their performance varied along the environmental gradients.

Overall, our results showed that the number of quadrats where the percentage of FDis differed significantly from that expected was negligible for all the null models and traits, thereby indicating that the null model algorithms accurately described the functional community structure (Table 1). However, evaluations of the performance of our null models showed that the frequencies of species occurrence generated under the abiotic null models were quite different from those observed in the community matrix (Fig. 1). In particular, we found a group of species that corresponded to those found most often where their frequencies of occurrence tended to be similar to the observed frequencies, whereas rare species (i.e., species present in less than 20%

quadrats) appeared in the null assemblages at frequencies similar to an unweighted random assembly, which were far larger than those observed. This suggests that the individual abiotic models of these rare species were very poor, and thus they entered the null assemblages almost at random as a simple proportion of the total regional number of species. In addition, the abiotic null model was also the worst at reproducing the composition of natural assemblages (Appendix 1), thereby suggesting that abiotic processes themselves are unable to completely explain the observed patterns, so other processes such as biotic interactions are necessary to better reproduce the community functional configuration (Cornwell & Ackerly, 2009; de Bello et al., 2012). In fact, when we analyzed the relationships among the SES of functional diversity (i.e., discrepancies between observed and expected) for each single trait and the multi-trait combination along conspicuous environmental gradients, we mostly detected significant relationships with the environmental gradients under the abiotic null model (Fig. 2). In particular, the largest FDisc values in absolute terms were found at both extremes of the elevational and solar radiation gradients, which suggests that other assembly mechanisms (probably the biotic interactions, as discussed in the following) are much more important in these parts of the gradients (Michalet et al., 2006).

In general, positive discrepancies between the observed and expected functional diversity (i.e., more functional diversity than expected) have been interpreted as evidence for trait divergence in plant communities, whereas negative discrepancies have been interpreted as trait convergence (de Bello, 2012; Mason, De Bello, Doležal, & Lepš, 2011; Swenson & Enquist, 2009). For instance, we found that high potential solar radiation values led to large negative discrepancies (i.e., convergence) in two critical functional traits: Hmax and SM (Fig. 2). Solar radiation is a proxy for energy input and it may negatively affect the performance of alpine plant species in terms of the water balance and evapotranspiration (Mooney, Hillier, & Billings, 1965; Ritchie, 1998). However, in the alpine vegetation belt of the Central Pyrenees where summer storms are frequent, similar to other temperate mountains, solar radiation normally exerts a positive effect on productivity by lengthening the effective growing season via early snowmelt and a higher energetic input (Körner, 2003). Previous studies of similar mountains have also detected a tendency to convergence in SM with increasing solar radiation (de Bello et al., 2013), and even convergence in plant height in early snowmelt zones (Venn, Green, Pickering, & Morgan, 2011). In our study, the increase in the FDisc values towards sunnier slopes (i.e., convergence in Hmax and SM) suggests that the assembly is not mediated by abiotic conditions because the null communities were generated using a mechanistic model with parameters that exclusively specify abiotic processes (Botta-Dukát & Czúcz, 2016; L. Chalmandrier et al., 2013).

Therefore, our results suggest that in relatively more benign conditions, the trait convergence patterns for these traits could be explained by competitive processes, which sort species with different competitive abilities (i.e., by excluding less competitive species) (Mayfield & Levine, 2010). It should be noted that the grasslands belonging to the *Festucion scopariae* alliance prefer sites with the highest solar radiation in the Pyrenees (Alonso, 2005), whereas in other conditions, it is likely that the species that dominate the community outcompete other functionally dissimilar plants that might enter the community.

The functional divergence (i.e., higher functional diversity than expected) of the Hmax, LT, and multi-trait combination increased with elevation (Fig. 2). According to previous studies, the mechanisms that induce greater functional dispersion are associated with two opposing processes: competition (MacArthur & Levins, 1967) or facilitation (Gross et al., 2013; Soliveres, Torices, & Maestre, 2012). The “stress-gradient hypothesis” suggests that facilitation will become prevalent over competition as environmental stress increases (Michalet et al., 2006), and thus facilitative processes are expected to increase with elevation due to extreme environmental conditions (Callaway et al., 2002; Loïc Chalmandrier et al., 2017).

We only found a similar effect of elevation on Hmax with the biotic null model (Fig. 2), where this can probably be explained by the effects of disturbance regimes on plant trait variation, which increases at low elevations in these mountains. Thus, species that lack suitable traits for persisting under grazing conditions would be removed from the community (de Bello, Lepš, & Sebastià, 2006; Díaz, Noy-meir, & Cabido, 2001; Ding, Zang, Letcher, Liu, & He, 2012), thereby decreasing the functional diversity. In fact, hemicryptophytes are the dominant plants in intensively managed pasture and they have similar plant sizes. Our results suggest that the biotic ecological rules were also unable to describe the observed functional patterns, at least for this plant functional trait. Overall, according to the relatively poor performance of the abiotic models, the problems with the biotic models, and the superior performance of the mixed models, we can conclude that both deterministic mechanisms operate simultaneously, where facilitation in the most stressful environments and competition in the most benign may become prevalent due to predicted shifts at the extremes of the environmental gradients.

In the last two decades, ecologists have increasingly investigated methods for understanding the processes that drive community assembly from a functional ecology perspective but no consensus has yet been reached regarding the most appropriate protocol for generating the null communities for comparison (Gotelli & Graves, 1996). In this study, we provided some insights into new theoretical and methodological advances in null modelling for

assessing the relative importance of the processes and mechanisms that underlie community assembly. Our approach demonstrates the importance of using appropriate null models that have clear connections with ecologically driven processes in order to successfully detect the underlying mechanisms that shape the functional structure of plant communities (de Bello, 2012). In particular, our results highlight the potential use of environmentally constrained null models to test the effects of biotic interactions such as facilitation or competition. Thus, our results indicate that biotic interactions are critical drivers of community assembly in alpine ecosystems at the extremes of the local ecological gradients where this type of community thrives. Our models are realistic but finding significant differences between the observed and expected functional patterns is rare, so a detailed exploration of the discrepancies between null assemblages and natural assemblages can provide insights into the prevalence and performance under field conditions of different assembly mechanisms or rules.

In this context, we highlight two important caveats for future studies, as follows. (1) It is important to emphasize the utility of null models for comparing patterns but inference of the community assembly mechanisms should also be considered because different processes could give the same results (Kraft et al., 2015). (2) We fixed the species richness at each site in our null models where we assumed that the carrying capacity of each site is different in terms of the function of the local ecological conditions, such as soil fertility and abiotic stress, because the regional pool is shared and there are no limitations on dispersal. Therefore, the detection of biotic processes could be blurred because the species richness is also an outcome of competitive interactions. We hope to inspire further studies that will contribute to the construction of a unified methodological framework for functional ecology analysis.

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Authors' contributions

JLA, MC, and AE conceived the ideas and designed methodology; JLA, DSP, ALL, AMS and AE collected the data; JLA and MC analyzed the data; JLA led the writing of the manuscript, with important contributions from all authors.

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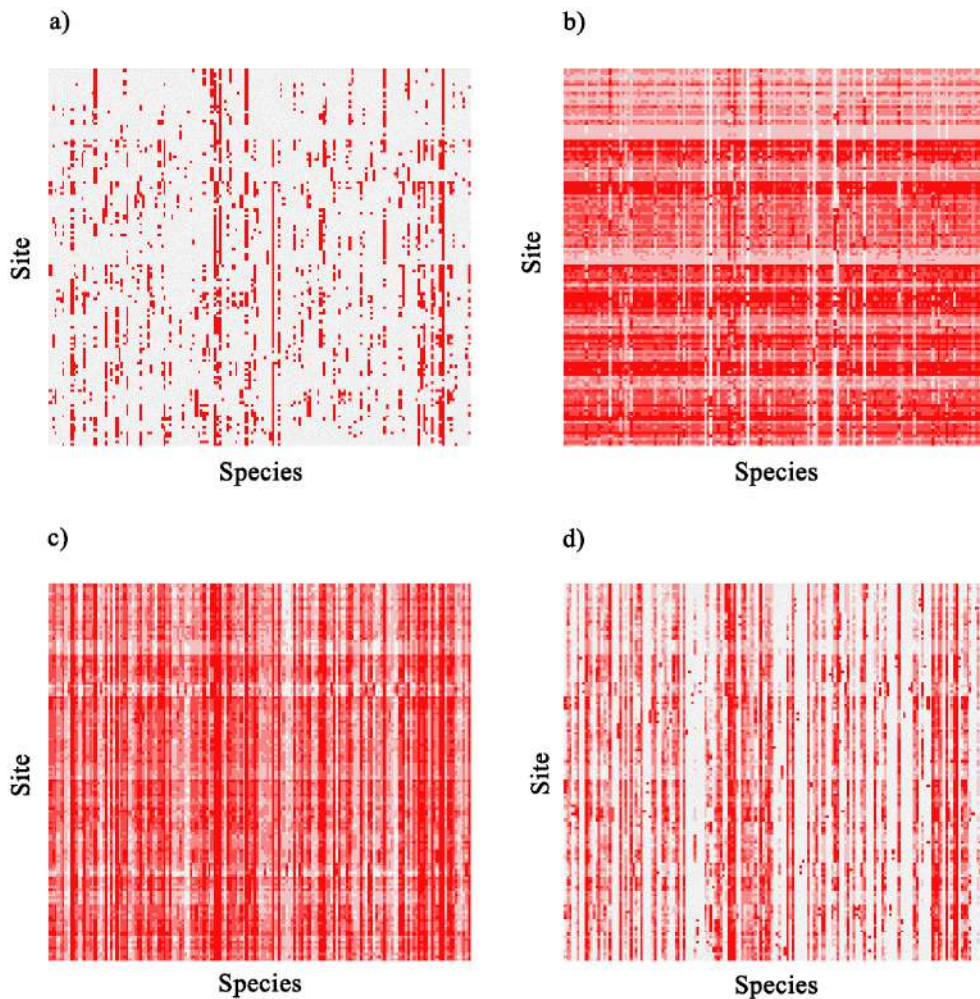
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Appendices

Appendix 1. Incidence matrix representations of: (a) the original data and the data generated under the (b) abiotic, (c) biotic, and (d) mixed abiotic–biotic null models. The intensity of the colour indicates the incidence for the average of 999 randomizations, except for the original data in the presence/absence matrix.



Chapter 4

**Biogeography, climate and biotic interactions
determine the interplay between functional, phylogenetic
and taxonomic diversities**



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Manuscrito inédito

Abstract

Disentangling the variation of interplay among diversity components along biotic and abiotic gradients may contribute to our understanding of community assembly processes. We assessed the interplay among functional (FD), phylogenetic (PD) and taxonomic diversity (TD) in three different mountain ranges with contrasting evolutionary histories (Europe/South America) and climate conditions (Mediterranean and Temperate climates) to know if the mechanisms implied in the assembly are similar among mountains. In each mountain region, we sampled the grasslands occurring above the local treeline, covering the complete elevation gradient where this ecosystem-type occurs. We sampled 830 quadrats and registered more than 200 species, which were characterized by 5 functional traits and by phylogenetic relatedness. We used species richness and mean pairwise distances (MPD) as a measure of TD, and FD and PD, respectively. Structural equation modeling tested the model that comprised the causal hypotheses about the relationships among FD, PD and TD and abiotic (elevation, potential solar radiation and soil nitrogen content) and biotic factors (plant-plant interactions). We found a high degree of idiosyncrasy with evident differences among mountains although some critical relationships were consistent across regions. The main consistent result was that increasing elevation affected functional and taxonomic diversity, which was generally reduced in the upper elevation limit. We also found a negative relationship between FD and TD in Guadarrama NP and in Ordesa-Monte Perdido NP. Our results suggest the strong environmental filtering processes that usually occur in alpine environments, together with a balance between competition and facilitation affected by variations in environmental conditions likely lead to the community assembly.

Introduction

Disentangling the underlying mechanisms driving the assembly of plant species in natural communities is critical for understanding the uneven distribution of species diversity across the Earth (Diamond 1975; Keddy & Weiher 1999; Gotelli & McCabe 2002). Abiotic conditions and plant-plant interactions are critical factors in determining species co-occurrence and species composition in natural communities (Keddy 1992; Chase & Myers 2011; HilleRisLambers et al. 2012). Traditionally, species richness and individual abundance distributions have been used to detect community assembly processes by using null models of known numerical properties (Rosenzweig 1995; Grytnes & Vetaas 2002; Willig et al. 2003). However, this perspective assumes that species are ecologically equivalent and evolutionary independent (Safi et al. 2011; Swenson 2011). So, during the last two decades, functional and phylogenetic perspectives have emerged as fruitful approaches for quantifying ecological and evolutionary processes on community assembly overcoming the inherent limitations of the so-called taxonomic approach.

Combining the distributions of species and their level of co-occurrence with community functional similarity between natural assemblages allow to identify assembly rules or other ecological mechanisms that taken together determine the composition of communities (Weiher & Keddy 1995; Diaz et al. 1998). The functional perspective of the community assembly suggests that biotic and abiotic determinants could act as ecological filters allowing species to enter into the community on the basis of their functional trait configuration (Cornwell & Ackerly 2009; Götzenberger et al. 2012). This implies that only species with the appropriate morphological, physiological, and phenological traits will be able, at least in probabilistic terms, to enter into the natural assemblages and successfully persist (Violle et al. 2007; Shipley et al. 2016). This plant trait-based framework has led over the last decades to a need of incorporating functional information in the studies of community assembly and lately the explicit consideration of the phylogenetic structure of the assemblages since most of the relevant functional traits have a evident evolutionary signal (Diaz et al. 1998; Webb et al. 2002; Pavoine & Bonsall 2011; Escudero & Valladares 2016). In addition, the use of the phylogenetic relatedness among species also allowed the explicit consideration of the historical processes underlying speciation and other events such as species diversification or migration in the assembly process (Davis et al. 2002; Webb et al. 2002; Hughes & Eastwood 2006). Furthermore, the quantification of the phylogenetic relationship among species has given information related to local-scale ecological

processes under the premise that closely related species are ecologically more similar (Webb et al. 2002; Hardy 2008; Mayfield & Levine 2010; Le Bagousse-Pinguet et al. 2017).

Nonetheless, the relationships among functional (FD), phylogenetic (PD) and taxonomic diversity (TD) on ecological communities have been seldom assessed (but see: Bernard-Verdier et al. 2013; Oliver et al. 2013; Dainese et al. 2015), and this may greatly enhance our ability to identify the mechanisms that lead local communities (Pavoine & Bonsall 2011; Oliver et al. 2013; Dainese et al. 2015). Plant trait-based ecology (Escudero & Valladares 2016; Shipley et al. 2016) suggests that a strong and positive correlation between FD and TD is expected when species functional uniqueness predominates in species traits (equally complementary: Petchey & Gaston 2002). This means that there is almost no functional redundancy among species, so each taxonomic label (i.e. species name) corresponds to a unique functional configuration. Emergence of these correlations between these two diversities might reflect the importance of niche complementarity as a mechanism of community assembly. In contrast, low levels of FD along with high levels of TD could suggest environmental filtering (Keddy 1992; Kraft & Ackerly 2010). On the other hand, the relationship between FD and PD could be structured according to the phylogenetic signal of the functional traits implied. That is, high FD values could lead to high PD values if phylogenetic conservatism prevails in the functional traits selected to estimate FD (Webb et al. 2002).

Disentangling the variation of the interplay between FD, PD and TD along biotic and abiotic gradients may contribute to our understanding of community assembly processes (Pavoine & Bonsall 2011; Oliver et al. 2013; Dainese et al. 2015). In this context, mountain ecosystems should be appropriate ecosystems to achieve this goal as they show strong and foreseeable environmental changes with elevation, a surrogate of climatic variations (Körner 2007; Sanders & Rahbek 2012). Even more, recent studies suggest that shifts in elevation and other abiotic variables such as solar radiation have important consequences not only in TD but also in FD and PD. For instance, elevation yields environmental filtering constraining FD (de Bello et al. 2013; Read et al. 2014), PD (Jin et al. 2015; Xu et al. 2017) and TD (Rahbek 1995; Cuesta et al. 2017), although other relationships have also been found and could be expected (Le Bagousse-Pinguet et al. 2017; López-Angulo et al. 2018). There are other critical abiotic determinants in high mountain environments such as total nitrogen in the soil, considered as the main limiting nutrient in alpine ecosystems (Sundqvist et al. 2014) and solar radiation (de Bello et al. 2013), which can generate heterogeneity at relatively fine spatial scales modifying climatic primary conditions (i.e. temperature) due to elevation. In addition, biotic interactions, especially positive ones, are known to play a key role in the processes governing community assembly in

high-mountains (Choler et al. 2001; Callaway 2007; Cavieres et al. 2014) leaving also detectable imprints on the functional and phylogenetic structure of the communities (Verdú & Valiente-Banuet 2011).

Although harsh alpine environments generally converge in community assembly processes throughout the world's mountains (e.g. facilitation: Callaway et al. 2002), some idiosyncratic features such as climate and evolutionary history can alter the prevalence of each assembly process (Safi et al. 2011). Thus, the regional species pool originated by biogeographical and evolutionary processes, together with the climate context and man-driven perturbations, determine community structure including species composition and the interplay among the different components of diversity. Therefore, to progress towards a unified framework, we need to assess the interplay among PD, FD and TD and their environment in different mountain ranges with a completely different evolutionary and biogeographic histories (Europe/South America), and with contrasted climatic conditions (Mediterranean and Temperate climates) within the same biogeographical region. The arising question is obvious: are the mechanisms implied in the assembly similar among mountains?

Here, we assess how several key abiotic and biotic determinants -elevation, total nitrogen in soil, potential solar radiation and biotic interactions- in each local assemblage (C-score: Stone & Roberts 1990; Dullinger et al. 2007) shape and affect the relationships among TD, FD and PD. Furthermore, in order to test to which extent these relationship depends on climate and biogeographic history, we compared the interplay among FD, PD and TD in three different mountain ranges with contrasting evolutionary histories and climate conditions.

Materials and Methods

Study sites

This study was conducted in three mountain ranges, with different climate and/or biogeographic history. (1) Sierra de Guadarrama National Park (Guadarrama NP, hereafter; 40°47' N, 4°0' W), in central Iberian Peninsula, which is characterized by a typical Mediterranean climate with intense summer droughts; (2) Ordesa-Monte Perdido National Park (42°40' N 0°03' E) in the central Pyrenees (in the north fringe of the Iberian Peninsula), within the same geographic region but with a temperate climate; and (3) the surroundings of Valle Nevado (33°20'S, 70°14'W) and Laguna del Maule (35°58'S, 70°30'W), in the central Chilean Andes, with a completely different regional species pool but also characterized by a Mediterranean-type climate. Mean annual temperature and annual precipitation are 6.5 °C and 1350 mm at 1894 m

a.s.l. respectively, in the central Iberian Peninsula (Navacerrada Pass weather station; 40° 47' N, 4° 00' W; 1894 m a.s.l.). In central Pyrenees, has a temperate climate without summer droughts since storms in summer are very frequent. Mean annual temperature and annual precipitation are 5°C and 1660 mm (Góriz weather Station; 42° 39' N, 00° 01' E; 2215 m a.s.l.) respectively. Finally, in the central Chilean Andes, mean annual temperature and annual precipitation are 6.5 °C (Cavieres et al. 2000) and 943 mm (Santibañez & Uribe 1990) respectively, at 2300 m a.s.l.

In each mountain region, we sampled grasslands occurring above the local treeline in snow-free zones such as windblown slopes and crests covering the complete elevational gradient where this ecosystem-type occurs. Elevation in our study ranged from 1890 to 2420 m in the central Iberian Peninsula, from 1650 to 2550 m in the central Pyrenees, and from 2064 to 3627 m a.s.l. in the in the central Chilean Andes. Dominant perennial vegetation in the three locations is generally patchily distributed with open areas. Dominant plants were grasses of the genus *Festuca* and *Poa*, together with creeping chamaephytes, perennial forbs and cushion-like plants.

Field sampling

We sampled 39 sites during June and July of 2011 in Guadarrama NP (central Spain), 20 sites during July of 2013 and 7 during July of 2014 in Ordesa-Monte Perdido NP (central Pyrenees), and 20 sites during January of 2014 in the central Mediterranean Andes. We established in each site a sampling plot of 20 x 20 m in relatively homogeneous vegetated areas considering a wide range of aspects and slopes along the local elevation gradient. Five 2.4 m x 2.4 m quadrats were established at the four-corners of the plot and a fifth in the center. This sample size is large enough to represent the variation of this type of communities (see Pescador et al. 2015). The central quadrat was thoroughly divided into 64 cells of 30 cm x 30 cm (8 x 8 cells). Each species percentage cover (%) was visually estimated at each quadrat and each cell. We used a grid size of 30 cm x 30 cm according to the average plant diameter (18 cm for Guadarrama NP and central Mediterranean Andes and 6 cm for Ordesa-Monte Perdido NP, authors' own unpublished data) which would reflect the real plant to plant interactions in the observed assemblage. Cell information was used to calculate the checkerboard score (C-score: Stone & Roberts 1990) in order to estimate plant to plant interactions (Dullinger et al. 2007). The C-score index quantifies the degree of aggregation for species co-occurrence. High C-score values indicate a tendency for species to spatially segregate which would reveal prevalence of competitive interactions, and low values of this index would indicate species aggregation and facilitative processes (Dullinger et al. 2007).

We measured in each plot, elevation and aspect using a GPS (Garmin Colorado-300, Garmin Ltd., Olathe, USA) and slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Aspect and slope values were used to calculate the potential solar radiation (Gandullo 1974). Elevation was standardized by subtracting the treeline elevation value from plot elevation in the Chilean Andes (see: López-Angulo et al. 2018) since the sampled sites were distributed in different latitudes and the treeline was locally well-conserved. We collected one soil sample (5 cm in diameter and 10 cm deep) in the four corners of each plot. Soil samples were collected from bare areas to reflect the variations linked to abiotic differences among sites (Mihoč et al. 2016). The soil estimates of the center quadrat were calculated as the average of the four quadrats at each site. Soil samples were air dried for one month and sieved through a 2 mm mesh. We measured soil total nitrogen content because it is considered one of the main limiting nutrients in alpine ecosystems (Sundqvist et al. 2014). Total soil nitrogen (mg N g⁻¹ soil) was determined on a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in the Nutilab/URJC lab after digestion with sulphuric acid and Kjeldahl's catalyst (Anderson & Ingram 1994).

Plant Functional Traits

Five functional traits were measured for the most abundant species in each mountain range (56 species (98% of the total) in Guadarrama NP, 96 (60%) species in Ordesa-Monte Perdido NP and 71 (67%) species in in the central Chilean Andes). These groups of species represented at least 80% of the accumulated cover of each quadrat which ensures a satisfactory description of functional community properties (Pakeman et al. 2007; Borgy et al. 2017), reaching 99% of the accumulated cover in Guadarrama NP, 94% in Ordesa-Monte Perdido NP and 87% in Central Chile. We measured five key functional traits that are expected to play a critical role in functional niche differentiation among species. (i) Maximum vegetative height (H_{max}, distance from the ground to the top of photosynthetic tissues) is correlated with above-ground biomass and represents a trade-off between competitive vigor (Cornelissen et al. 2003) and protection by snow cover (Körner 2003). (ii) Plant size (PS, canopy area projection) is a surrogate of the photosynthetic biomass and it is directly related to accumulated resources (Pescador et al. 2015). (iii) Specific leaf area (SLA, ratio of one-sided area of a fresh leaf divided by its dry mass) is correlated with relative growth and photosynthetic rates (Cornelissen et al. 2003). (iv) Leaf dry matter content (LDMC, oven-dried mass of a leaf divided by its fresh water-saturated leaf mass) is usually well correlated with resource investment in leaf tissues and with resistance to physical hazards (Cornelissen et al. 2003). (v) Leaf thickness (LT) is related to nutrient acquisition and resistance to wind (Choler 2005). All these traits were measured in at

least ten different healthy and well developed individuals per species, following the standard methodology of Cornelissen et al. (2003) with the exception of plant size, which was calculated as $PS = \pi \cdot L \cdot S / 4$ (Pescador et al. 2015), where L is the longest diameter and S is the shortest diameter perpendicular to the former one for each plant. In addition, trait data for the species of Ordesa-Monte Perdido NP (central Pyrenees) was completed with information from the LEDA traits database (Kleyer et al. 2008).

DNA sequencing and phylogenetic analyses

We constructed a phylogenetic tree using two barcoding loci (rbcL and matK) in order to estimate the phylogenetic diversity. We used a species pool composed of species found in the communities together with similar species from Torres del Paine NP (Chile). Available species sequences from GenBank were downloaded (122 matK and 117 rbcL sequences) and the rest (771 sequences) were obtained in the laboratory. Fresh leaves from three individuals per species were collected and were lately dry-stored in silica-gel for 1 month. Genomic DNA was isolated and extracted using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA).

PCR amplifications of the rbcL barcode were performed in 25 μ L containing a reaction mixture of 2.5 μ L of Taq buffer 2 mM with $MgCl_2$, 1 μ L of dNTP Mix (0.4 mM), 1.25 μ L of reverse and forward primer, 1.25 U Taq DNA Polymerase (Biotools, Madrid, Spain) and 2 μ L of genomic DNA. The matK barcode was amplified by puReTaq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Uppsala, Sweden). Primers for PCR, sequencing and PCR cycling conditions used in this study followed Lopez-Angulo et. (2018). The subsequent products were clean-up using the ExoSap purification kit® (USB Corporation, Cleveland, OH, USA) and sequenced by MacroGen Inc (Seoul, South Korea). Sequences were initially aligned using MAFFT online v. 7, and minor manual adjustment of the alignments was necessary only for the matK barcoding with Mesquite version 2.6. Maximum likelihood (ML) gene trees were calculated by the R-package Phangorn (Schliep 2011) using the GTR+G+I model and 100 bootstrap replicates.

Diversity metrics and statistical analyses

We used species richness as a measure of TD, and mean pairwise distances (MPD) weighted by species abundances to estimate the functional and phylogenetic diversity of each quadrat. Distances among coexisting species were calculated using the Gower distance index to estimate FD and the cophenetic distance to estimate de PD. Before calculating the FD, we conducted a principal component analysis (PCA) using all the traits measured to control for

correlations among traits and to define a multidimensional trait space for each mountain region (Devictor et al. 2010). Two to three axes were needed to explain at least 85% of the variance (Table 1). The Gower matrix to calculate FD was estimated according to the selected PCA axes. Calculation of MPD was performed using the melodic function (de Bello et al. 2016).

Table 1. PCA loadings and the proportion of variance explained by each axis for the Principal Component Analyses with the 5 traits measured in each location.

	Guadarrama NP		Ordesa-Monte Perdido NP			Central Mediterranean Andes		
	PC1	PC2	PC1	PC2	PC3	PC1	PC2	PC3
Hmax	-0.17			-0.27		0.61	-0.11	-0.47
Plant Size	-0.24			-0.72	-0.67	0.52		-0.35
SLA	0.64	-0.43	-0.33	0.40	-0.40	-0.12	0.67	-0.32
LDMC	-0.70	-0.32	-0.66	-0.47	0.51	0.54		0.73
Leaf thickness		0.84	0.67	-0.18	0.37	-0.22	-0.73	-0.15
Proportion of Variance	0.52	0.34	0.43	0.33	0.13	0.45	0.33	0.17
Cumulative Proportion	0.52	0.86	0.43	0.76	0.89	0.45	0.78	0.95

We determined the phylogenetic signal for each plant trait (and the selected PCA components) to confirm phylogenetic niche conservatism when we found significant relationships between FD and PD. We tested the phylogenetic signal with the Pagel's λ using a Brownian motion model of trait evolution (Pagel 1999), with the subset of species found in each mountain region. Pagel's λ was quantified using the 'phylosig' function in the Phytools package in R.

Structural Equation Modeling

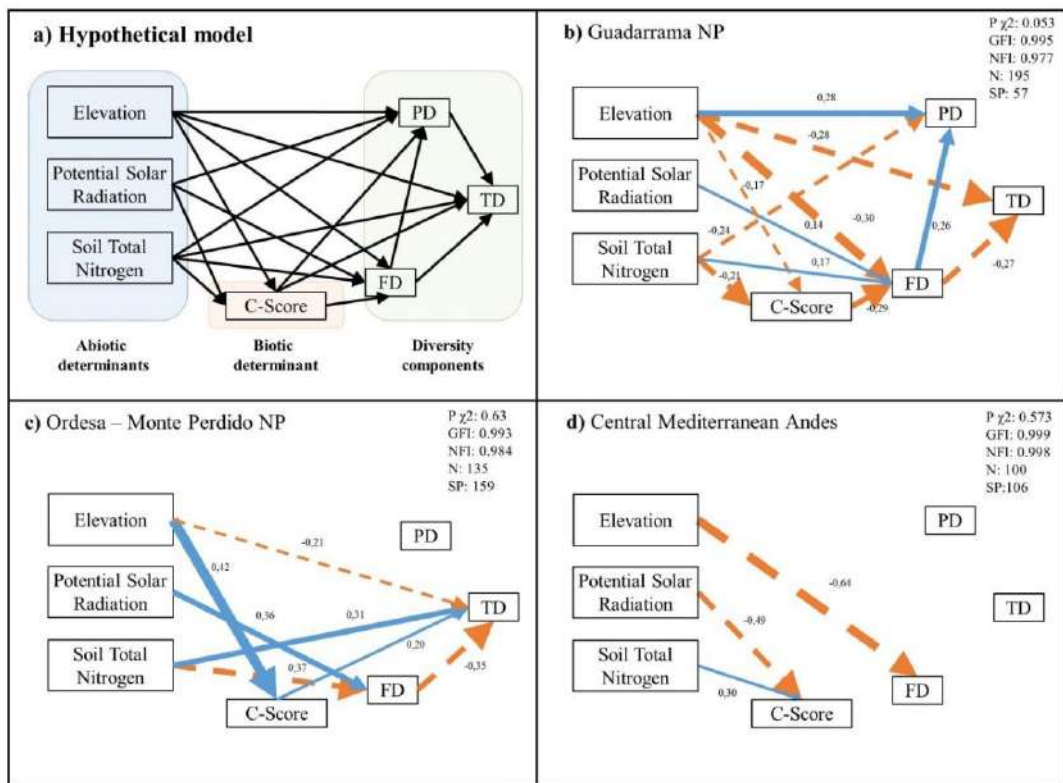
The model we tested comprised the causal hypotheses about the relationships among FD, PD and TD and abiotic (elevation, potential solar radiation and soil nitrogen content) and biotic factors (plant-plant interactions). Our theoretical model proposes that each diversity component, FD, PD and TD, can respond to abiotic conditions and to the intensity of plant - plant interactions (Fig. 1a) independently. It is possible to find shifts in the relationships because each

component of diversity reflects different community aspects and provides information about different assembly processes. We hypothesized that FD would depend on abiotic and biotic factors because the selected traits are known to respond to them in alpine ecosystems (Dainese et al. 2015; Pescador et al. 2015). In the same way, if selected plant traits are phylogenetically conserved, PD would respond rather similarly to such environmental factors (Cavender-Bares et al. 2004; Swenson et al. 2007). If the causal paths for both diversity components were different, we could suggest that environmental determinants affecting PD are probably reflecting the response of other unmeasured traits with phylogenetic signal. TD is expected to be directly influenced by FD and PD, although these relationships will depend on the degree of functional redundancy in the selected traits (FD) and in the unmeasured traits (PD) (Petchey & Gaston 2002). However, regardless of indirect effects on TD of environmental forces through FD and PD, we expect elevation, nitrogen in soil and biotic interactions to be critical determinants structuring species richness (TD) directly. This implies that TD can be affected by ecological determinants both directly or indirectly through FD and PD. Finally, we considered that environmental conditions could directly affect prevalence of plant interactions and consequently indirectly affect the interplay among components of diversity. Since the relationships among environmental factors and the diversity components could be specific for each mountain range, the model was evaluated for each region separately. Fest will be used if necessary, in order to detect paths with different behaviors among mountain ranges.

To test the theoretical model, we used a Structural Equation Modelling (SEM). SEMs allow us to test causal links established in an initial hypothetical framework, comparing the variance-covariance structure that describes the relationships among all variables. SEMs takes into account the constraints imposed by the theoretical hypotheses with the observed variance-covariance structure (for more details, see: Mitchell 1992; Iriondo et al. 2003; Maestre et al. 2005; Grace 2006). If discrepancies are small, we can assume that the observed pattern is compatible with our hypotheses. The three abiotic factors represented the exogenous variables, whereas the biotic variable (plant-plant interactions) and the three diversity components corresponded to endogenous variables (Fig. 1a). Standardized estimates of path coefficients were obtained using the maximum likelihood method because it is robust against certain deviations of multinormality (Shipley 2000). We used standardized coefficients to interpret scaling relationships among variables. Total soil nitrogen content for Ordesa-Monte Perdido NP was log-transformed to reach normality. The discrepancies between observed and expected covariance matrices were first assessed by a chi-square goodness-of-fit statistic (χ^2). In this case, P-values above 0.05 indicate that the observed and the modelled covariances were not significantly

different, suggesting adequate model fit. Since this test is prone to several statistical errors, especially when the sample size is large, we also used two additional measures of the goodness of fit: the comparative fit index (CFI) and the Bentler and Bonett's normed-fit index (NFI) (Iriondo et al. 2003). Before analyses and to be sure that our data sets were multinormal we calculated the variance inflation factor (VIF) for each variable. We incorporated all variables in the models since all VIF values were < 4 (Petraitis et al. 1996). SEM were conducted using Amos v18 (SPSS, Chicago, Illinois, USA).

Figure 1. Path diagram (and structural equation model results) representing hypothesized causal relationships among the components of diversity (TD, FD and PD) and their abiotic and biotic determinants. a) Theoretical model, models tested for b) Guadarrama NP in central Spain, c) Ordesa-Monte Perdido NP in central Pyrenees and d) in central Chilean Andes. Positive effects, solid blue lines; negative effects, broken orange lines. Arrow widths are proportional to adjacent standardized path coefficients. Path coefficients non significantly different from zero are omitted. Goodness-of-fit statistics ($P \chi^2$, GFI and NFI) and sample size (N) are provided at the upper-left corner of each diagram.



Results

We registered 57 species in Guadarrama NP ($n=195$ quadrats), 159 species in Ordesa-Monte Perdido NP ($n=135$ quadrats) and 106 species in the central Chilean Andes ($n=100$ quadrats). The average number of species per quadrat was $10.9 (\pm 2.6 \text{ SD})$ in Guadarrama NP and $11.2 (\pm 4.5 \text{ SD})$ in the central Chilean Andes, being the richest mountain Ordesa-Monte Perdido NP with an average of $18.8 (\pm 7.7 \text{ SD})$ species per quadrat. The five most frequent species in Guadarrama NP (*Festuca curvifolia*, *Rumex angiocarpus*, *Jurinea humilis*, *Sedum brevifolium* and *Jasione crispa* subsp. *centralis*) occurred at least in a 67% of the quadrats, whereas in Ordesa-Monte Perdido NP (*Thymus praecox*, *Koeleria vallesiana*, *Galium pyrenaicum*, *Festuca gautieri* subsp. *scoparia* and *Helictotrichon sedenense*) and in the central Chilean Andes (*Poa denudate*, *Trisetum preslei*, *Hordeum comosum*, *Phacelia secunda* and *Bromus setifolius*) these species were registered in 36% and 32% of the quadrats, respectively. The central Chilean Andes was characterized by a strikingly nutrient poor soils regarding total nitrogen (0.6 mg g^{-1}) in comparison to the other mountain ranges ($>3 \text{ mg g}^{-1}$, see Table 2).

Table 2. Mean values of the endogenous and exogenous variables included in the structural equation model. TD: Taxonomic diversity. PD: Phylogenetic diversity. FD: Functional diversity.

Mountain range	TD	PD	FD	C-score	Elevation	Potential solar radiation	Soil total nitrogen (mg g ⁻¹)
Guadarrama NP	11	0,373	0,303	46,10	2127	0,739	3,710
Ordesa-Monte Perdido NP	19	0,363	0,219	47,15	2144	0,649	3,279
Central Mediterranean Andes	11	0,348	0,270	40,08	2834 *(884)	0,814	0,616

*Standardized elevation is shown in parentheses

The causal models (see Fig 1) were significant but, in contrast to our expectations, they were very different, so we did not need to conduct a multisample analysis. The model for Guadarrama NP provided a good fit to observed data because it had a non-significant χ^2 ($\chi^2=7.74$, $DF=1$, $P=0.053$) and the values of NFI and GFI were higher than 0.90 (Fig 1b). Soil

nitrogen and potential solar radiation had positive effects on FD while the effects of elevation and the C-score were negative. However, in spite of positive relationships between FD and PD, suggesting phylogenetic conservatism, PD was influenced by soil nitrogen and elevation in a way contrary to FD (Fig. 1b). TD was negatively affected by elevation whereas the interplay between FD and TD was also negative.

The model for Ordesa-Monte Perdido NP received high statistical support, as suggested by non-significant χ^2 values ($\chi^2=3.45$, $DF=1$, $p=0.063$) and by values of NFI and GFI higher than 0.9, indicating that field data adjusted to the theoretical model (Fig. 1c). In contrast to the results for the Guadarrama's model, in this case the strength of the model was mainly due to the strong relationship between the environmental predictors and TD (Fig. 1c). TD was positively affected by soil nitrogen and C-score while elevation had a negative effect on TD. FD was positively influenced by solar radiation and negatively by soil nitrogen. The negative relationship between FD and TD found in the Guadarrama model was again observed here (Ordesa-Monte Perdido NP model). However, no other relationship between biotic or abiotic variables and PD was found (Fig. 1c).

Finally, the model for the central Chilean Andes was also fitted as indicated by the non-significant χ^2 values ($\chi^2=3.18$, $DF=1$, $p=0.573$) and the NFI and GFI values, which were again far above 0.90 (Fig. 1d). However, in this case an exclusive significant relationship (elevation and FD) was detected among predictors and community diversity. In spite of the strong causal relationships between soil nitrogen and potential solar radiation with the surrogate of biotic interactions (C-score) (Fig. 1d) no other relationships with diversity components were detected.

We found significant phylogenetic signal for every plant trait in central Chilean Andes. In Guadarrama NP and Ordesa-Monte Perdido NP, significant phylogenetic signal was found in all plant traits except for specific leaf area (SLA; Table 3). For each of the PCA axes obtained from the plant functional traits only in Guadarrama NP were significant and relatively high, indicating phylogenetic signals (Table 3).

Table 3. Phylogenetic signal in 5 functional traits calculated for the subsets of species found in each mountain region according to Pagel's λ metric. The significance is shown as *: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; *** $p < 0.001$.

Guadarrama NP	Ordesa-Monte Perdido NP	Central Mediterranean Andes
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Hmax	0.86	***	0.37	***	0.24	***
Plant Size	0.99	***	0.69	***	0.84	***
SLA	0.31		0.00		0.56	*
LDMC	0.87	***	0.60	***	0.66	***
Leaf thickness	0.67	*	0.94	***	0.59	*
PC1	0.78	***	0.88	***	0.76	***
PC2	0.69	*	0.51	***	0.49	
PC3			0.14		0.04	

Discussion

Here we evaluated a causal model of relationships among different diversity components (TD, FD and PD) to both biotic and abiotic local environment conditions across different mountain ranges with different evolutionary history, disturbance regime, and climatic conditions. Our results confirmed that the theoretical model adequately described the observed data in the three mountain ranges (Fig. 1b-d). Even more, it provided empirical evidences that highlight the direct relationships among the studied abiotic and biotic factors with the different components of diversity. Although numerous studies have revealed that abiotic determinants shape diversity in terms of taxonomic, functional or phylogenetic properties (Bernard-Verdier et al. 2013; Oliver et al. 2013; Dainese et al. 2015), our study represents a first attempt to define how the abiotic environment together with the role played by plant-plant interactions, which are modulated in turn by the same abiotic environment, determine the interplay among the TD, FD and PD in alpine communities. Our approach also reveals that under certain circumstances the indirect relationships with the ecological determinants may be different to those reflecting direct links. Worth to note also that our hypothetical model was compatible with the three contrasting data sets although the causal links varied among regions suggesting important idiosyncratic differences.

We found that FD was strongly influenced by various environmental variables, and it was the unique diversity component that responded to environment in the three mountain ranges (Fig. 1b-d) supporting the extended idea that the assembly processes at fine spatial scales is determined by the functional configuration of the species involved (Keddy 1992; Weiher & Keddy 1995). Moreover, FD influenced directly TD in both Spanish mountain ranges, and it also influenced PD in Guadarrama NP, reinforcing the importance of the role of the FD in the

community assembly. Other studies, however, have shown different signs in the relationships of FD and the other components of diversity. Pillar & Duarte (2010) found that phylogenetic structure is the responsible for structuring FD following the temporal perspective in which the evolutive relationships go first in the assembly process. Others authors, proposed that TD influence the other components of diversity (Flynn et al. 2011; Pavoine et al. 2013). Our results are congruent with our hypothesis that FD is the diversity dimension primarily related to ecological sorting pressures. It facilitates detecting the imprints of the assembly processes in the communities as long as the appropriate traits are measured (Shipley et al. 2016). Nevertheless, TD was the component of diversity most affected by the environmental determinants in Ordesa – Monte Perdido NP and it was also restricted by elevation in Guadarrama NP, suggesting that species richness captures other important aspects of diversity and assembly. Thus, species and functional traits could provide different and complementary information, and combining them, our potential to identify the processes that structure biological communities patently increases (Díaz & Cabido 2001; Mouchet et al. 2010; Bernard-Verdier et al. 2013). Additionally, we found few significant relationships in which PD was involved. In accordance with previous studies, this suggests that PD is a poor indicator of assembly processes (Pavoine et al. 2013; Gerhold et al. 2015).

In spite of the good fit of the observed data as a whole to the constraints imposed by our model, we found a high degree of idiosyncrasy with evident differences among mountains. Indeed, we found that some relationships even shifted from positive to negative from one mountain range to another. This suggests that some relationships are strongly context-dependent, making it difficult to draw general conclusions so we should yield specific conclusions for each particular region. First, elevation was negatively and positively related to the C-score metric in Guadarrama NP and in Ordesa – Monte Perdido NP, respectively. Additionally, total soil nitrogen affected positively the FD in Guadarrama NP whereas in Ordesa – Monte Perdido NP total nitrogen content negatively influenced FD (Fig 1b). In the case of the co-occurrence patterns, we expected an interspecific aggregation with increasing environmental severity (elevation) in all mountain ranges due to the prevalence of facilitation (Choler et al. 2001; Callaway et al. 2002). However, the role of facilitation decreased with increasing elevation in Ordesa - Monte Perdido NP. We speculated that in this Temperate mountain without summer drought the environment conditions were particularly harsh at the top collapsing the facilitative interactions, as suggested by Soliveres et al. (2012) in extremely arid environments. It is also worth to comment that other mechanisms, such as increasing heterogeneity with elevation cannot be ruled out as an additional explanation for segregation of species (Dullinger et al. 2007). On the

other hand, the large discrepancies found in the relationships between total soil nitrogen content and FD agree with other studies (Pakeman et al. 2011; Mason et al. 2012; Spasojevic & Suding 2012). It is well known that plant diversity responds to soil fertility in an unimodal way (Grime 2006) so, the sign of the underlying relationship may depend on the segment of the hump in which we were working. Therefore, the relationship between FD and total nitrogen may represent the ascending and descending sides of the curve in Guadarrama NP and at Ordesa- Monte Perdido NP, respectively. Taken all together our results suggest that the dominant assembly mechanisms could vary from environmental filtering under Mediterranean climate (Grime 1973) to various competition-related mechanisms in temperate climate conditions Temperate region (Grime 1977; Weiher et al. 1998). Even more, differences in nitrogen content in the soil can be mediated through other drivers such as cattle grazing (Afzal & Adams 1992; Liu et al. 2016) that alters the concentration of nitrogen affecting the functional diversity and structure of the communities (de Bello et al. 2006). In any case, grazing in the studied mountains is absent or simply residual which suggests that herbivory by domestic cattle is irrelevant.

Despite our results showed high variability among regions, we found constant patterns that indicated that some processes could be generalized. The main consistent result was that increasing elevation significantly affected functional and taxonomic diversity, which was generally reduced in the upper elevation limit. This result is one of the most commonly reported patterns for alpine environments (Rahbek 1995; de Bello et al. 2013; Read et al. 2014; Cuesta et al. 2017). Severity of environmental conditions usually increases with elevation, causing a reduction in the range of trait values and thus, limiting the number of the plant species established in such stressful environments (Weiher & Keddy 1995; Cornwell et al. 2006). It is noteworthy that in Guadarrama NP the increase in elevation generated an increase in PD opposite to the decline in FD, in spite of PD was positively correlated with FD, which was consistent with the strong phylogenetic signal found in the considered functional traits (Table 3). Although a decrease in PD have generally been described in the literature with increasing elevation (Bryant et al. 2008; Graham et al. 2009; Machac et al. 2011) specially in plants (Li et al. 2014; Xu et al. 2017), discrepancies between the functional and phylogenetic structures have also been reported in high-elevation grasslands in the European Alps (Dainese et al. 2015). A potential explanation for this striking result is the hypothesis posed by Valiente-Banuet & Verdú (2007), who showed that facilitation intensity increased in harsher environmental conditions and it was associated to higher PD. In our study, the increase in facilitation intensity was supported by the fact that elevation led to low levels of the C-score values, that can be interpreted in terms of a higher

prevalence of positive interactions among plants with increasing altitude (Dullinger et al. 2007; Schöb et al. 2013).

Additionally, we found negative relationships between FD and TD in Guadarrama NP and Ordesa-Monte Perdido NP regions (Fig. 1 b-c). This relationship suggests that ecological redundancy may occur in the richest assemblages (Naeem 1998; Loreau 2004). These findings contrast with the intuitive hypothesis that higher FD values are associated to higher species richness (Petchey & Gaston 2002). Similar to our results, de Bello et al. (2009) found an increase in functional redundancy associated to an increase in species diversity in alpine pastures in the Catalanian Pre-Pyrenees. Our results highlight that the functional volume of plant traits was occupied by a few species and when species richness increased, the new species were not functionally different from those already present (Díaz & Cabido 2001). This strong niche overlap among species can be interpreted as the result of a strong abiotic filtering on the whole alpine community related to harsh environmental conditions. Particularly interesting was this consistency of the relationship across regions sharing regional species pool and similar evolutionary histories. It is important to note that the mean pairwise functional distance-based metrics (unaffected by richness) such as the MPD, can decrease when a redundant species enters into the community whereas sum of distances based-metrics (i.e. Faith's Index) always increase with richness (Díaz & Cabido 2001; Petchey & Gaston 2002; Swenson 2014).

Disentangling the interplay among the diversity components and their variation across different mountain ranges with different evolutionary history, and climatic conditions, provides knowledge about the mechanisms that shape community structure in alpine plant communities. A part from the strong environmental filtering processes that usually occur in alpine environments, a balance between competition and facilitation affected by variations in environmental conditions is likely to lead the community assembly. However, extrapolating such local processes to other species pools must be taken with caution due to the idiosyncratic nature of the observed relationships in the study. Our results highlight the importance of considering the different components of diversity (TD, FD and PD). Although functional traits are expected to respond directly to environmental drivers, our results encourage using taxonomic (almost forgotten in later years) and phylogenetic information as well. Although species richness and phylogenetic patterns do not encompass all aspects of functional community structure (Mouchet et al. 2010), our study highlights that TD and PD capture different and complementary information about community assemblage processes.

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Discusión general



La identificación de procesos deterministas como las denominadas reglas de ensamblaje (Diamond, 1975) en comunidades de plantas ha sido un tema prioritario en ecología de comunidades casi desde el albor de la Ecología (Clements, 1916). Esta Tesis aborda la búsqueda de las reglas ecológicas de ensamblaje en comunidades naturales de plantas de alta montaña, así como la identificación de los principales mecanismos responsables de estructurar la diversidad en dichos ecosistemas. Se ha prestado especial atención a algunas de las limitaciones que restringen el progreso hacia la obtención de un marco global que explique la coexistencia a todas las escalas espacio-temporales; lo que se ha denominado Teoría de Coexistencia (Chesson, 2000; Hart, Usinowicz, & Levine, 2017). La construcción de un marco teórico global nos permitiría entender cómo se produce el ensamblaje de las comunidades y de los determinantes que conducen a la convivencia de las especies. Desafortunadamente la obtención de este marco permanece todavía en su infancia (Swenson, 2011). Hasta ahora, existe un amplio consenso de que el ensamblaje de las comunidades está mediado por procesos puramente estocásticos junto con otros deterministas. Estos últimos se rigen por reglas que depende de las constricciones que imponen las condiciones ambientales y las interacciones del medio biótico en las comunidades (Chase, Kraft, Smith, Vellend, & Inouye, 2011; Escudero & Valladares, 2016; Götzenberger et al., 2012; HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Vellend et al., 2014; Wilson, 1999).

A pesar de tener un marco esbozado continúan existiendo numerosas discrepancias a la hora de encontrar las reglas de ensamblaje, incluso cuando se buscan en los mismos ecosistemas y regiones. Algunos de los elementos que limitan el avance hacia un marco unificado tienen que ver aspectos puramente metodológicos como los que se producen a la hora de fijar la escala de estudio (Chase, 2014; Harmon & Harrison, 2015; McGill, 2010; Münkemüller et al., 2014) o aquellos que están relacionados con el uso de metodologías analíticas desfasadas y que no son capaces de discernir entre mecanismos causantes de los patrones. En otras ocasiones, el uso de métricas basadas en información taxonómica las cuales tratan a todas las especies como evolutivamente independientes y ecológicamente equivalentes limitan el entendimiento de los mecanismos que subyacen a los patrones de diversidad (Petchey & Gaston, 2006; Swenson, 2011; Webb, Ackerly, McPeck, & Donoghue, 2002). Así, la discusión general de la presente tesis está por tanto centrada en dos aspectos principales: (1) cuáles son las reglas ecológicas de ensamblaje que prevalecen en la configuración de las comunidades de plantas de alta montaña; y (2) en qué medida se han salvado las limitaciones de las que adolece el marco actual y que permiten un avance en la teoría de la coexistencia de especies.

Aunque sabemos que los procesos subyacentes al ensamblaje pueden actuar a diferentes escalas espaciales y temporales, actualmente no existe un consenso que determine la escala concreta a la que los patrones de diversidad en las comunidades responden a los procesos ecológicos de ensamblaje (Burton, Mladenoff, Clayton, & Forrester, 2011; Chalmandrier et al., 2017; Leibold et al., 2004; Münkemüller et al., 2014). Así, no conocemos la escala espacial ideal que se debería usar para detectar los distintos mecanismos de ensamblaje (Magurran, 2004). Conscientes de esta limitación, propusimos una aproximación multi-escalar desde el punto de vista espacial definiendo al menos tres escalas organizadas de manera jerarquizada y se estudió el efecto de varios factores los cuales se esperan que actúen a distinta escala sobre la estructura de la diversidad en las comunidades. Así esperamos que la altitud afecte a la diversidad de especies a una escala grande, mientras que otros componentes de la heterogeneidad ambiental, como la insolación o la fertilidad del suelo, esperamos que lo hagan a escala más pequeña, siendo las interacciones bióticas las que en principio deberían de actuar a las escalas más pequeñas donde se producen los contactos directos entre las plantas (Leibold et al., 2004).

Tanto en el Capítulo 1 como en el Capítulo 2, se usó un enfoque multi-escalar para esclarecer cómo los factores bióticos (i.e., estimando la interacción a nivel comunidad con un índice de co-ocurrencia como el c-score) y los abióticos (altitud, la insolación y la fertilidad del suelo) afectan a la diversidad taxonómica (DT), a la diversidad funcional (DF) y la diversidad filogenética (DP). Como esperábamos, encontramos distintos resultados cuando las relaciones entre las variables ambientales y las distintas facetas de la diversidad fueron estudiadas a las distintas escalas, es decir, el efecto de algunos factores solo se produjo a escalas específicas. Esto corrobora la idea de que es necesario considerar el enfoque multi-escalar para dilucidar los mecanismos que estructuran las diversidades de plantas (Burton et al., 2011; Leibold et al., 2004); también en el caso de comunidades de alta montaña (Münkemüller et al., 2014). Concretamente, cuando estudiamos la diversidad taxonómica de los Andes chilenos y sus determinantes, encontramos un efecto significativo de la altitud en varias métricas como la riqueza, un conocido estimador de diversidad alfa, y la diversidad beta a la escala mayor (parcela), mientras que estas métricas de DT solo fueron influidas por el componente biótico a las escalas más pequeñas (Capítulo 1). Es frecuente encontrar variación en los patrones altitudinales de diversidad cuando varía el tamaño de la escala espacial de estudio (Nogués-Bravo, Araújo, Romdal, & Rahbek, 2008; Rahbek, 2005). En nuestro caso, parece que a escalas más pequeñas el efecto de la altitud sobre la diversidad taxonómica se difumina, posiblemente como consecuencia del mayor efecto que tienen otras variables a esta escala, como por ejemplo las interacciones bióticas. En este sentido se sabe que la facilitación puede producir incrementos de la diversidad

en condiciones muy duras (Cavieres et al. 2015) o lo contrario una prevalencia de la competencia en determinadas zonas puede producir caídas de la riqueza. Consistentemente, el efecto de las interacciones bióticas sobre los otros componentes de la diversidad (el funcional y el filogenético) en las comunidades de plantas de los Andes mediterráneos chilenos, solo fue detectable a las escalas más pequeñas al igual que ocurrió con el efecto de la fertilidad del suelo (Capítulo 2). Particularmente interesante es la consistencia que muestra el efecto del c-score (i.e., interacciones bióticas) influyendo sobre los tres componentes de la diversidad solo a pequeñas escalas. Esto coincide con lo esperado, ya que los procesos ecológicos que involucran interacciones de especies ocurren principalmente a escalas pequeñas (de Bello et al., 2013; Götzenberger et al., 2012) y por tanto, estos procesos solo se pueden detectar cuando se considera la escala espacial que comprende los vecindarios donde las plantas interactúan.

Merece la pena resaltar la consistencia que mostraron algunas de las relaciones estudiadas a través de las tres escalas, como la relación entre la fertilidad del suelo y la DT (Capítulo 1), o la interacción entre la altitud y la insolación con las DF y la DP (Capítulo 2). Los resultados sugieren cierta homogeneidad ambiental asociada a los nutrientes del suelo, ya que los efectos de muestras tomadas a escala pequeñas se proyectaron a escalas mayores aumentando la DT a todas las escalas (Eilts, Mittelbach, Reynolds, & Gross, 2011; Reynolds, Mittelbach, Darcy-Hall, Houseman, & Gross, 2007). En el caso de la interacción entre la altitud y la insolación, esperábamos una exacerbación de su efecto sobre la DF y la DP a escalas grandes. Sin embargo, la alta variación en la temperatura que se produce localmente a lo largo del gradiente altitudinal y en función de las orientaciones, hace que sus efectos se mantengan constantes a través de las escalas espaciales sin que lleguen a difuminarse por el efecto del otro factor que actúe con mayor intensidad a escalas pequeñas. Es impactante ver como la interacción es relevante cuando cada uno de los factores actúa preferentemente a escalas diferentes, la altitud siguiendo ese conocido patrón de descenso de 0,6 grados de temperatura con cada 100 metros de ascenso y la insolación variando el *input* energético dentro de cada altitud.

Por otro lado, cabe destacar como el efecto de los predictores tanto abióticos como bióticos, fue distinto cuando consideramos la DT (Capítulo 1), la DF y la DP (Capítulo 2), con la salvedad de la fertilidad del suelo, la cual aumentó los tres componentes de la diversidad de las comunidades en los Andes. En primer lugar, hay que tener en cuenta que los datos no provienen de las mismas zonas de muestreo exactamente, dado que la DF y la DP fue estudiada exclusivamente en las zonas mediterráneas debido a la ausencia de información sobre los rasgos vegetales de las plantas del sur de Chile, lo que limita en cierta medida la comparación. Otros factores de distinta naturaleza podrían tener implicaciones directas y participar en alguna medida

en estas discrepancias. Por un lado, cada componente de la diversidad refleja diferente información de la comunidad, y por tanto, pueden responder a los factores ambientales de distinta forma reflejando distintos procesos de ensamblaje (Devictor et al., 2010; Pavoine & Bonsall, 2011). Por otro lado, hay que sumar que la aproximación metodológica que se usó para analizar la estructura de la DF y la DP no fue la misma que la que se usó para analizar la DT. En el primer capítulo se modelizaron los índices taxonómicos en bruto, mientras que en el segundo, los dos componentes de la diversidad (DF y DP) fueron enfrentados a las correspondientes diversidades esperadas bajo un modelo nulo, con lo cual, se modelizó una propiedad emergente que está determinada por mecanismos que se excluyen en la aleatorización y que son los responsables de generar las desviaciones del modelo nulo (de Bello, 2012; Gotelli & Graves, 1996).

El modelo nulo usado en el capítulo 2 es un modelo que genera comunidades esperadas distribuyendo al azar las incidencias de la matriz de datos observada, pero manteniendo fija la riqueza de especies observada en las comunidades y la tasa de ocupación de las especies en todo el sistema de estudio (Gotelli & Entsminger, 2003). La elección de este modelo nulo tiene sentido ecológico, ya que el número de especies de una comunidad está relacionado con el pool regional, las limitaciones a la dispersión, la capacidad de carga de territorio y la competencia (Connor & Simberloff, 1979; Gotelli, 2000). Por el otro lado, aquí proponemos que la tasa de ocupación de la especie debe verse como una estima de la probabilidad de ocurrencia que tienen las especies particulares en función de su biología en la zona de estudio (Gotelli, 2000; Jonsson, 2001). Por tanto, si la propiedad observada, en este caso la diversidad funcional, no es diferente de lo que de lo que cabría esperar bajo el modelo nulo, indicaría la inferencia en la configuración de la comunidad del proceso de ensamblaje que subyace a las reglas del modelo. De lo contrario, si se encuentran patrones diferentes de los generados por el modelo nulo se puede inferir la acción de algún mecanismo no conocido pero responsable de generar estos patrones. El problema viene a la hora de discernir entre los mecanismos causantes de las discrepancias de diversidad funcional (de Bello, 2012).

Analizar la variación de las desviaciones funcionales a lo largo de gradientes ambientales puede facilitar la interpretación de los patrones funcionales. Por ejemplo, en el Capítulo 2, la dispersión funcional mostró valores relativamente altos sugiriendo sobredispersión de los rasgos vegetales de la comunidad en los dos escenarios que probablemente presenten las condiciones más estresantes de la zona de estudio: en cotas altas poco insoladas (condiciones más frías) y en altitudes bajas pero altamente irradiadas por el sol (condiciones más cálidas y secas). Por otro lado, en los sitios donde la insolación suaviza el efecto de la altitud, el patrón funcional predominante fue el de la agrupación de especies que tienen un perfil de rasgos similar. Este

último patrón, el de la agrupación de rasgos, ha sido generalmente atribuido al efecto del filtrado abiótico que producen las condiciones estresantes en las comunidades (Cavender-Bares, Keen, & Miles, 2006; de Bello et al., 2009). Sin embargo, este patrón fue encontrado en los sitios que presentaban condiciones más suaves mientras que donde el filtrado ambiental podía esperarse, encontramos el patrón opuesto. De este modo, el análisis de la estructura de la diversidad funcional a lo largo de gradientes ambientales nos ha permitido sugerir la prevalencia de las interacciones bióticas (Pausas & Verdú, 2010). Son muchos los estudios que han demostrado la gran importancia de las interacciones bióticas como determinante del ensamblaje (Butterfield & Callaway, 2013), especialmente en sistemas alpinos (Anthelme, Cavieres, & Dangles, 2014; Mitchell et al., 2009; Schöb, Armas, Guler, Prieto, & Pugnaire, 2013). Los resultados sugieren que la facilitación dominó en las zonas con condiciones abióticas más limitantes en el sistema de estudio (Butterfield & Callaway, 2013; Callaway et al., 2002; Gross et al., 2013; Pistón, Armas, Schöb, Macek, & Pugnaire, 2015), mientras que en las zonas más benignas, es la dominancia competitiva la principal fuerza en determinar el ensamblaje (MacArthur & Levins, 1967; Michalet et al., 2006).

Si bien es cierto que los patrones encontrados mediante esta metodología no permiten establecer una relación causal entre la acción de un determinado mecanismo y un patrón ecológico, las evidencias son poderosas a falta de una evaluación experimental (Juliano & Lawton, 1990). Sin embargo, el uso de modelos nulos más realistas que representan mejor la acción de procesos de ensamblaje facilita para dar un salto cualitativo en la búsqueda de mecanismos que estructuran las comunidades ecológicas. Así en el capítulo 3, usamos un enfoque novedoso para incorporar la acción de las reglas ecológicas de ensamblaje en los modelos nulos. Concretamente, comparamos la estructura funcional de las comunidades observadas y la estructura funcional esperada bajo el efecto de reglas de ensamblaje que subyacen a determinantes abióticos, bióticos o a la acción simultánea de ambos, para revelar su papel en el ensamblaje de la comunidad. De los tres modelos nulos utilizados, el modelo abiótico fue el peor a la hora de reproducir la composición de ensamblajes naturales. Además, las discrepancias entre la diversidad funcional observada y esperada, para cada rasgo y para la combinación multi-trait, variaron a lo largo de los gradientes ambientales cuando las comunidades esperadas se generaron con el modelo nulo abiótico (Capítulo 3). Estos resultados sugieren que los procesos abióticos por si solos no son capaces de explicar completamente los patrones observados, y por lo tanto, procesos que involucran interacciones bióticas pueden ser los responsables de reproducir la configuración funcional de la comunidad (Cornwell & Ackerly, 2009; de Bello et al., 2012). Más concretamente los patrones generados con un modelo nulo que

introduce las especies en las comunidades nulas considerando de forma simultánea las preferencias ambientales de las especies (biótico) y su patrón de co-ocurrencia (biótico) son casi idénticos que los que se han tomado en el campo.

Estos resultados encontrados en el Pirineo central, del mismo modo que los hallados en los Andes mediterráneos chilenos, sugieren que las interacciones bióticas son un determinante crítico del ensamblaje de la comunidad en los ecosistemas alpinos, cuya importancia se ve exacerbada en los extremos de dos gradientes ambientales en los que aparecen estas comunidades, que tienen que ver con variaciones de temperatura como son la insolación y la altitud. Sin embargo, estas variables influyen de distinta manera a las comunidades de plantas alpinas debido a características idiosincráticas propias de cada región, y como resultado dan lugar a distintas estructuras funcionales de las comunidades en los mismos puntos de los gradientes ambientales. Así, en las montañas chilenas influenciadas por el clima mediterráneo, la sequía estival propia de este clima (Cavieres, Badano, Sierra-Almeida, Gómez-González, & Molina-Montenegro, 2006; Sierra-Almeida, Reyes-Bahamonde, & Cavieres, 2016) reduce el periodo de actividad vegetativa particularmente con mayor intensidad a bajas altitudes. Esto hace que las condiciones adversas no aumenten de manera lineal con la altitud en montañas mediterráneas como puede ocurrir en las montañas templadas de Pirineos, sino que las condiciones desfavorables pueden darse de manera unimodal (Cavieres et al., 2006; Giménez-Benavides, Escudero, & Iriondo, 2007; Mihoč et al., 2016), dando como resultado, por ejemplo, patrones de riqueza de especies cuyos valores máximos se dan en altitudes intermedias (Capítulo 1) en lo que podríamos llamar el dominio medio de la comunidad (mid-domain) (Colwell & Lees, 2000).

A pesar de la importancia que tiene el clima en definir la prevalencia de las reglas de ensamblaje de nuestras comunidades, en el Capítulo 4 hemos podido comprobar que sus efectos no tienen por qué ser generales, y que otros factores idiosincráticos pueden afectar a los procesos que subyacen en el ensamblaje de las comunidades. Así pues, las relaciones del ambiente con la comunidad y las interacciones que ocurren entre las especies que las forman, van a depender entre otros factores del *pool* regional de especies del cual provienen estas especies (Harrison & Cornell, 2008), de la longitud de los gradientes estudiados (Grytnes, 2003) y de las perturbaciones de origen antrópico (Billings 1973; Olff & Ritchie 1998), lo que dificulta establecer generalidades. Por ejemplo, en la Sierra de Guadarrama las comunidades de plantas se ven limitadas por la altitud de la montaña y no por las condiciones climáticas, por lo que los patrones de diversidad observados pueden ser una pequeña parte del patrón que se esperaría con el incremento de la altitud.

Para concluir, esta tesis sugiere que la estructura de las comunidades de plantas alpinas subyace a las reglas ecológicas de ensamblaje, tanto bióticas y como abióticas. De este modo, los principales mecanismos que determinan la estructura de las comunidades de plantas de alta montaña en nuestras zonas de estudios son un complejo equilibrio entre competencia y facilitación que se produce en respuesta a la variabilidad en las condiciones ambientales, junto con el filtrado ambiental que producen las bajas temperaturas de alta montaña. En ocasiones, a pesar de encontrar los mismos patrones de ensamblaje en regiones con distinto clima, los mecanismos responsables pueden diferir. En otras ocasiones las relaciones entre la comunidad y sus determinantes pueden ser totalmente idiosincráticos llegando a encontrar relaciones completamente opuestas. El efecto de los determinantes bióticos y abióticos en la diversidad taxonómica ve incrementada su intensidad a escalas espaciales específicas debido a que los procesos subyacentes al ensamblaje actúan a diferentes escalas espaciales. Por ejemplo, la altitud influye a la diversidad taxonómica a mayor escala que las interacciones bióticas, cuyo efecto se detecta a las escalas finas donde las interacciones entre plantas se dan.

Los resultados de esta tesis sugieren que al menos en resoluciones espaciales pequeñas, las interacciones bióticas son un factor crítico del ensamblaje de las comunidades del centro de Pirineos, que dejan una huella detectable en la estructura funcional de rasgos como la altura máxima de la planta o el peso de las semillas. Así, el uso de modelos nulos que representan la acción de reglas abióticas simulando comunidades a partir de constricciones ambientales abióticas presentan un gran potencial para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia. Por otro lado, la evaluación de la dispersión funcional a lo largo de múltiples gradientes de estrés ayuda a interpretar los patrones encontrados, dado que diferentes mecanismos pueden producir los mismos patrones (p.e. la facilitación y la competencia pueden generar divergencia funcional). Además, considerar interacciones entre gradientes, ya sean aditivas o sinérgicas, pueden revelar nuevas perspectivas para los procesos de ensamblaje de las comunidades. Por ejemplo, la interacción entre la altitud y la insolación produce divergencia funcional y filogenética como resultado de las interacciones facilitadoras donde las condiciones son más estresantes. Por el contrario, cuando las condiciones son más suaves, el dominio de unas pocas especies que son más competitivas podría conducir a patrones de convergencia funcional.

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Conclusiones generales



De los resultados obtenidos en esta tesis doctoral se pueden extraer las siguientes conclusiones generales:

- La estructura de las comunidades de plantas alpinas subyace a las reglas ecológicas de ensamblaje, tanto bióticas y como abióticas. Un complejo equilibrio entre competencia y facilitación producido en respuesta a la variabilidad en las condiciones ambientales, junto con el filtrado ambiental que producen las bajas temperaturas de alta montaña, son los principales mecanismos que determinan la estructura de las comunidades de plantas de alta montaña en nuestra zona de estudio.
- Los mecanismos responsables de causar y mantener los patrones de diversidad taxonómica pueden diferir en regiones sometidas a distinto régimen climático en los Andes Chilenos. La respuesta unimodal de la riqueza al gradiente altitudinal parece estar influenciado por la sequía estival la cual se intensifica a baja altitud, mientras que en los Andes Sub-antárticos donde la sequía es despreciable, parece que la facilitación que producen las especies nodriza sobre otras especies puede subir ligeramente el número de especies en las comunidades a cotas intermedias donde abundan estas especies y el estrés no llega a ser extremadamente fuerte.
- El efecto de los determinantes bióticos y abióticos en la diversidad taxonómica ve incrementada su intensidad a escalas específicas. La respuesta de la comunidad a la altitud prácticamente fue detectable a la escala de parcela, mientras que el efecto de las interacciones bióticas solo fue patente a escalas pequeñas donde las plantas interactúan.
- El estrés en las montañas mediterráneas chilenas es intenso en ambos extremos del gradiente altitudinal debido a la existencia de gradientes opuestos como son el de temperatura y humedad. Además, la radiación solar puede atenuar o exacerbar la dureza ambiental asociada al gradiente altitudinal. En consecuencia, la interacción entre estos factores produce divergencia funcional y filogenética como resultado de las interacciones facilitadoras donde las condiciones son más estresantes. Por el contrario, cuando las condiciones son más suaves, el dominio de unas pocas especies que son más competitivas podría conducir a patrones de convergencia funcional.

- La diversidad filogenética proporciona información relevante cuando los rasgos seleccionados no tienen señal filogenética e incluso responden en el mismo sentido a los determinantes ambientales.
- Al menos en resoluciones espaciales pequeñas, las interacciones bióticas son un factor crítico del ensamblaje de las comunidades en los ecosistemas alpinos del centro de Pirineos. El uso de modelos nulos que representan la acción de reglas abióticas ensamblando las comunidades nulas a partir de constricciones ambientales, presentan un gran potencial para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia.
- La evaluación de la dispersión funcional a lo largo de múltiples gradientes de estrés ayuda a interpretar los patrones encontrados, dado que diferentes mecanismos pueden producir los mismos patrones (p.e. la facilitación y la competencia pueden generar divergencia funcional). Además, considerar interacciones entre gradientes, ya sean aditivas o sinérgicas, pueden revelar nuevas perspectivas para los procesos de ensamblaje de las comunidades.
- Se debe tener precaución al extrapolar procesos de ensamblaje que ocurren en sistemas alpinos particulares a otros ambientalmente similares debido alto grado de idiosincrasia que hay en las relaciones entre el entorno y la estructura de la comunidad. Si bien es cierto, hay relaciones tan potentes que pueden ser generalizadas a lo largo del planeta como es la disminución de la riqueza de especies con la altitud, al menos en el tramo final del gradiente donde el número de especies que son capaces de sobrevivir a tales condiciones extremas caen bruscamente.

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