

Introducción al Análisis Espacial de Datos en Ecología y Ciencias Ambientales: Métodos y Aplicaciones

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Efectos escala-dependientes de la abundancia de semillas y la estructura del hábitat en la depredación post-dispersiva de dos especies de matorral mediterráneo

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RESUMEN

La depredación de semillas es una interacción ecológica capaz de afectar a la composición de las comunidades vegetales, al determinar las abundancias relativas de propágulos de especies de plantas con distinta capacidad competitiva. La probabilidad de depredación de las semillas depende en gran medida de sus rasgos especí-

ficos, pero también del contexto espacial donde las semillas son dispersadas, en función de factores como la propia densidad de semillas o la estructura del hábitat. La heterogeneidad espacial en la cantidad de semillas y en la estructura del hábitat varía en función de la escala, por lo que es esperable que el efecto de esos factores sobre la depredación sea escala-dependiente. En este estudio evaluamos el efecto de la abundancia de semillas dispersadas y la estructura del hábitat sobre la tasa de depredación por roedores de dos especies de matorral mediterráneo, *Berberis vulgaris* subsp. *australis* y *Juniperus communis* a distintas escalas espaciales. Mediante un Análisis de Coordenadas Principales de Matrices de Vecinos (ACPMV), desglosamos la variación espacial de la depredación a distintas escalas y generamos valores predichos de depredación, que fueron relacionados con la abundancia de semillas y la estructura del hábitat. Encontramos diferencias significativas entre especies en la tasa neta de depredación. La tasa de depredación fue más predecible a escala espacial amplia que a escala fina. La relación entre la depredación y la cantidad de semillas o la estructura del hábitat varió en función de la especie y de la escala. Únicamente un parámetro estructural del hábitat, la cobertura arbórea, se relacionó positiva y simultáneamente con la tasa de depredación en las dos especies a la escala más amplia.

15.1. INTRODUCCIÓN

La depredación post-dispersiva de semillas es una causa principal de pérdidas reproductivas para muchas plantas (Hulme 1998, Hulme y Benkman 2002). Las diferencias en depredación entre especies coexistentes en un mismo hábitat pueden tener consecuencias importantes en términos de estructuración de las comunidades vegetales, especialmente cuando éstas conducen a diferencias en el reclutamiento de propágulos entre especies con distintas capacidades competitivas (Janzen 1971, Crawley 1992, Hulme 1998, García *et al.* 2005a). Muchas de estas diferencias interespecíficas están causadas por rasgos intrínsecos de las semillas, como el tamaño (Blate *et al.* 1998, Moles *et al.* 2003), el grosor de la cubierta (Blate *et al.* 1998), la proporción pericarpo/endocarpo (Moles *et al.* 2003, García *et al.* 2005a) o la presencia de sustancias químicas de defensa (Kerley y Erasmus 1991, Kollmann *et al.* 1998). Además, la probabilidad de supervivencia de las semillas de una especie puede depender de factores extrínsecos, relacionados con las características del contexto en el que son dispersadas las semillas, como la densidad de semillas dispersadas (Hulme 1994) o las características estructurales del hábitat (Rey *et al.* 2002). A través de su influencia en el comportamiento de los depredadores, estos factores contribuyen a generar plantillas de probabilidad de depredación altamente heterogéneas en el espacio, cuya forma influye directamente en el resultado demográfico y

comunitario de la mortalidad de propágulos. Por ejemplo, una mayor depredación bajo las plantas fuentes de semillas, motivada por la acumulación de las semillas dispersadas, determina patrones específicos de reclutamiento distancia-dependientes que contribuyen a la coexistencia local (Janzen 1971, Connell 1971, Hyatt *et al.* 2003). También el potencial de reclutamiento específico y la coexistencia se ven afectados por el papel de la fisionomía del hábitat cuando los depredadores concentran su actividad en determinados rodales o microhábitats (diferentes al dosel de las plantas madre) donde las semillas son movilizadas de forma diferencial por los vectores de dispersión (Schupp y Fuentes 1995, Jordano y Herrera 1995, García *et al.* 2005b).

La heterogeneidad espacial, tanto de los patrones de depredación como de los factores que los modulan, puede ser interpretada en términos de escala espacial (Kollmann 2000, García *et al.* 2005b). Por ejemplo, la abundancia de semillas dispersadas puede mostrar mayores diferencias espaciales a escalas pequeñas que a escalas grandes, mientras que la depredación puede mostrar un patrón inverso al estar condicionada preferentemente por factores diferentes a la densidad de semillas (Kollmann 2000, García y Houle 2005, García *et al.* 2005b). Estas diferencias de escala entre la abundancia de propágulos y los sucesivos factores de mortalidad de los mismos pueden determinar, de hecho, el resultado demográfico en términos de reclutamiento en las poblaciones de plantas (Schupp 1992, García *et al.* 2005b). A pesar de su importancia teórica, no existen estudios empíricos que comparen la heterogeneidad espacial en la tasa de depredación y en sus factores condicionantes principales desde perspectivas pluriescales, de forma que pueda determinarse a qué escalas influyen los distintos factores sobre la probabilidad de depredación. En este trabajo, utilizamos una aproximación pluriescalar espacialmente explícita para evaluar los patrones de depredación postdispersiva en dos especies de matorral de montaña mediterránea. En concreto, abordamos las siguientes preguntas:

- i) ¿Existen diferencias entre especies en la tasa neta de depredación y en la distribución espacial de la depredación?
- ii) ¿Puede explicarse la distribución espacial de la depredación en función de la abundancia de semillas y de las características estructurales del hábitat?
- iii) ¿Depende de la escala espacial y de la especie de semilla el efecto de la abundancia de semillas y de las características del hábitat en la depredación?

15.2. MATERIALES Y MÉTODOS

15.2.1. Área de estudio y selección de especies

El presente estudio se llevó a cabo durante el otoño-invierno de 2005-2006, en el Barranco del Espinar, dentro de los límites del Parque Nacional de Sierra Nevada (1900 m s.n.m., 37° 5.51' N, 3° 27.57' W). La vegetación de la zona está compuesta por un bosque autóctono de *Pinus sylvestris* L. var. *nevadensis* Christ en su cota altitudinal máxima, con matorrales oromediterráneos productores de fruto carnoso, principalmente agracejo (*Berberis vulgaris* subsp. *australis* Boiss.), enebro (*Juniperus communis* L.) y majuelo (*Crataegus monogyna* Jacq.), y de fruto seco como *Ononis aragonensis* Asso., *Genista versicolor* Boiss., *Erinacea anthyllis* Link., *Astragalus granatensis* o *Vella spinosa* (ver descripción en García *et al.* 2000a). El clima es de montaña mediterránea con una precipitación media anual de 818 mm. (promedio 1990-2006) concentrada en primavera y otoño, con veranos cálidos y secos e inviernos fríos y nevados. Los suelos son calcáreos (cambisoles y regosoles; Delgado *et al.* 1989).

Las especies seleccionadas para el estudio de depredación fueron *Juniperus communis* (*Juniperus* en adelante) y *Berberis vulgaris* (*Berberis* en adelante). Se escogieron estas dos especies por las siguientes razones: i) muestran un elevado grado de cobertura dentro de la zona (*Berberis* 16,13% y *Juniperus* 6,28%); ii) son productoras de fruto carnoso y coinciden fenológicamente en el período de maduración y dispersión (septiembre-diciembre), son dispersadas por el mismo gremio de vertebrados frugívoros, sobre todo zorzales y mirlos (*Turdus* sp.) que consumen los frutos enteros y dispersan las semillas intactas en sus excrementos, y su representatividad en la lluvia de semillas comunitaria es alta (13,63% y 10,82% del total de semillas ornitócoras dispersadas, *Berberis* y *Juniperus* respectivamente); y iii) estudios experimentales previos de depredación (García 2001, Matías *et al.* 2008) les otorgan valores moderados de probabilidad de depredación, lo que facilita representar los gradientes de heterogeneidad espacial de forma más nítida. El ratón de campo (*Apodemus sylvaticus*) es el principal depredador de semillas de estas especies leñosas en la localidad de estudio. Estudios previos no mostraron evidencias de consumo o retirada de semillas por otro tipo de depredadores, como hormigas o aves (Hulme 1997, García *et al.* 2000b, García 2001, Matías *et al.* 2007).

15.2.2. Estructura de muestreo

El marco espacial para el análisis de las interacciones fue un transecto lineal de 825 x 20 m, establecido a principios de octubre de 2005 a lo largo de una zona límite forestal altitudinal superior de un pinar de *Pinus sylvestris* var. *nevadensis*. El transecto se dispuso siguiendo la trayectoria más rectilínea posible, para evitar el solapamiento entre unidades de muestreo contiguas. La diferencia altitudinal máxima entre puntos del transecto fue menor de 200 m. El transecto se dividió en 165 parcelas contiguas alternas de 5 x 10 m, en cuyo interior se se marcaron otras dos estaciones de muestreo de 2 x 2 m en su eje central (Fig. 15.1). Todas las estaciones de muestreo ($n = 330$) fueron georreferenciadas a partir de su centroide, con un sistema arbitrario de coordenadas XY, que consideraba como punto 0,0 el vértice superior izquierdo de la primera parcela.

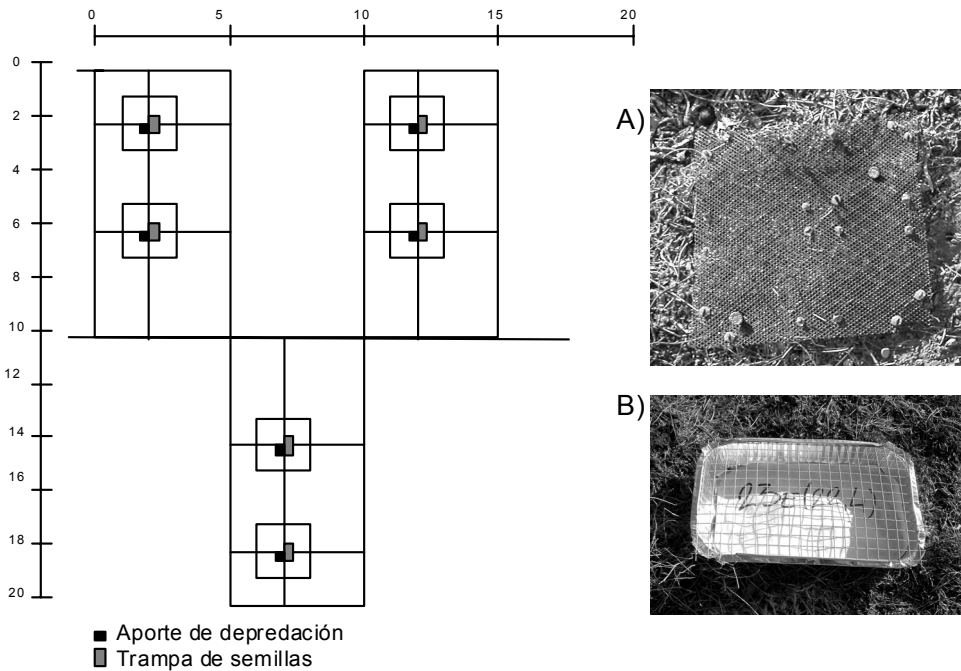


Figura 15.1. Diseño de muestreo dentro de cada parcela de 5 x 10 m, y las estaciones de muestreo de 2 x 2 m dentro de cada parcela. En cada estación de muestreo se colocó una trampa de semillas (A) y un aporte experimental de semillas para cuantificar la depredación (B).

15.2.2.1. *Características fisionómicas del hábitat*

En cada unidad de muestreo se registraron, entre el 1 y el 7 de octubre de 2005, las siguientes variables: i) porcentaje de cobertura (estima visual) de cada especie leñosa, distinguiéndose especies de fruto carnoso y de fruto seco, dentro de la estación de muestreo; ii) porcentaje de cobertura total de leñosas; iii) porcentaje de cobertura rocosa y de suelo mineral; y iv) altura media (5 medidas aleatorias dentro de la estación de muestreo) y máxima de la vegetación (en el punto más alto).

15.2.2.2. *Abundancia de semillas dispersadas*

La abundancia de semillas dispersadas por aves se cuantificó mediante trampas de semillas. En el centro de cada estación de muestreo se dispuso una trampa de semillas consistente en una bandeja de aluminio de 28 x 18 x 5 cm (superficie 0.042 m²), clavada al suelo y cubierta por una rejilla de 1 cm de luz de malla (Fig. 15.1). La rejilla permitió el paso de las semillas de los excrementos de las aves, pero evitó la depredación por roedores. Las trampas se colocaron entre el 1 y el 7 de octubre de 2005, se revisaron mensualmente recolectando su contenido y se retiraron en marzo de 2006. El contenido individualizado de cada trampa fue trasladado al laboratorio, contabilizándose el número de semillas por trampa de las distintas especies productoras de fruto carnoso presentes en la zona y consumidas por los frugívoros.

15.2.2.3. *Depredación post-dispersiva de semillas*

La depredación de semillas por roedores se estimó mediante aportes controlados de semillas. En cada estación de muestreo se colocó un aporte de semillas de *Berberis* y *Juniperus*, consistente en una rejilla plástica de 15 x 15 cm y 1 mm de poro clavada la suelo, sobre la que se pegaron con pegamento termofusible 10 semillas de cada especie focal, dispuestas alternas formando una espiral centrípeta (Fig. 15.1). El pegamento otorga una fijación suficiente para que las semillas no sean arrastradas por la lluvia o el viento y a la vez permite que sean retiradas por los roedores (ver García *et al.* 2005a, Matías *et al.* 2007 para metodología similar). Los aportes se revisaron pasados 90 días, apuntándose el número de semillas intactas, comidas (con marcas de mordiscos, vacías de contenido pero mostrando el resto de la cáscara) y desaparecidas en cada aporte. Para cada estación de muestreo se calculó la tasa de depredación de cada especie como la proporción de semillas depredadas respecto al total de semillas de cada especie en el aporte.

15.2.3. Análisis de datos

Se utilizó un Análisis de Coordenadas Principales de Matrices de Vecinos (ACPMV, Borcard & Legendre 2002, Borcard *et al.* 2004, Capítulo 2), que permitió desglosar la varianza espacial de la depredación de semillas a distintas escalas espaciales y relacionar dicha varianza desglosada con distintas variables ambientales. A partir de la estructura de muestreo del transecto, con 330 puntos de muestreo distribuidos regularmente, se obtuvieron 247 vectores de coordenadas principales. Para identificar aquellos vectores capaces de recoger la variabilidad espacial de la tasa de depredación de semillas, se realizó, para cada especie focal, un análisis de regresión múltiple considerando como variables independientes todos los vectores de coordenadas principales y como variable respuesta la tasa de depredación. Los vectores con un coeficiente de correlación parcial significativo ($P < 0.05$) se repartieron en tres escalas espaciales establecidas de forma equitativa: Macroescala, vectores significativos entre el vector 1 y el 68; Mesoescala, vectores entre el 69 y el 165; y Microescala, vectores entre 166 y 247. Posteriormente, se repitieron los análisis de regresión múltiple con los vectores seleccionados dentro de cada escala para generar submodelos espaciales correspondientes a cada escala, a partir de los cuales se calcularon los valores predichos de la tasa de depredación a las distintas escalas espaciales. Finalmente, se evaluó el efecto de la abundancia de semillas y de las características fisionómicas del hábitat sobre la variación espacial de la tasa de depredación de semillas a distintas escalas. Para ello se realizaron, para cada especie focal y para cada escala espacial, análisis de regresión múltiple considerando como variables predictoras la abundancia de semillas y las características fisionómicas del hábitat, y, como variables respuesta, los valores predichos de depredación de semillas de cada submodelo espacial.

15.3. RESULTADOS

Las especies estudiadas presentaron tasas de depredación significativamente diferentes, siendo mayor en *Juniperus* que en *Berberis* (Prueba de muestras emparejadas, $t = 2,35$; $p = 0,019$) (Fig. 15.2). Los análisis de regresión múltiple considerando los 247 vectores de coordenadas principales frente a las tasas de depredación de *Juniperus* y *Berberis*, identificaron 40 vectores significativos que explicaron el 56% de la variación espacial de la tasa de depredación de *Ju-*

niperus, y 24 vectores significativos que explicaron el 43% de la variación espacial en el caso de *Berberis*. Estos vectores se repartieron en tres escalas espaciales, acaparando la macroescala la mayor parte de la variabilidad espacial predecible de la tasa de depredación de ambas especies (Fig. 15.3). La representación de las tasas de depredación predichas por los submodelos espaciales a las tres escalas consideradas se muestra en la Figura 15.4. El efecto de la abundancia de semillas y las características fisionómicas del hábitat sobre la tasa de depredación dependió de la especie focal y de la escala espacial (Tabla 15.1). Tan sólo una variable fisionómica, la cobertura arbórea, tuvo un efecto similar (positivo) en las dos especies focales y a la misma escala (macroescala). El efecto de la abundancia de semillas dispersadas difirió entre especies, siendo negativo y a mesoescala para *Juniperus*, pero positivo y a macroescala para *Berberis*. La altura media y la cobertura de matorral mostraron un efecto positivo y a macroescala, pero la altura media sólo significativo para *Juniperus* y la cobertura de matorral para *Berberis*. La cobertura de rocas es el único factor que mostró efectos sobre la intensidad de depredación a microescala, y sólo en el caso de *Juniperus*, en la que muestra también efecto a macroescala.

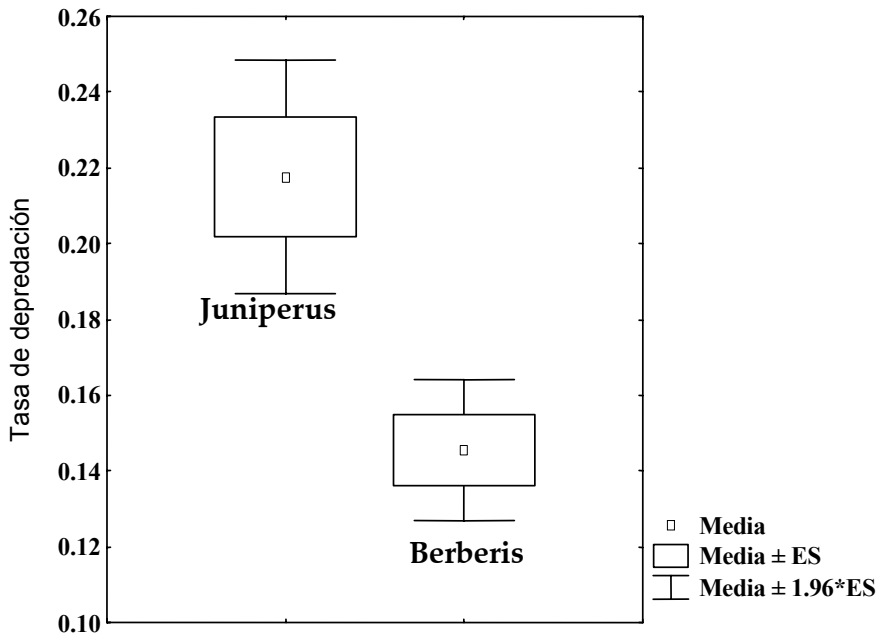


Figura 15.2. Proporción (media, + ES, + 1,96 ES) de semillas despregadas de *Juniperus* y *Berberis*; $n = 3300$ para cada especie.

Tabla 15.1. Tabla resumen de análisis de regresión múltiple considerando como variable respuesta la tasa de depredación predicha por los submodelos espaciales a distintas escalas y como variables predictoras la abundancia de semillas y las características del hábitat, para las dos especies focales. FC = fruto carnoso y FS = fruto seco.

Variable Respuesta	Escala	R ²	Factor	P	Signo interacción
Depredación <i>Juniperus</i>	Macroescala	0,145	Semillas dispersadas	0,165	n.s.
			Cobertura arbórea	0,004	+
			Altura Media	<0,001	+
			Matorral FC	0,856	n.s.
			Matorral FS	0,995	n.s.
			Cobertura rocas	<0,001	-
	Mesoescala	0,033	Semillas dispersadas	0,002	-
			Cobertura arbórea	0,333	n.s.
			Altura Media	0,463	n.s.
			Matorral FC	0,866	n.s.
			Matorral FS	0,451	n.s.
			Cobertura Rocas	0,337	n.s.
	Microescala	0,051	Semillas dispersadas	0,670	n.s.
			Cobertura arbórea	0,092	n.s.
			Altura Media	0,376	n.s.
			Matorral FC	0,822	n.s.
			Matorral FS	0,428	n.s.
			Cobertura Rocas	0,001	-
Depredación <i>Berberis</i>	Macroescala	0,135	Semillas dispersadas	0,002	+
			Cobertura arbórea	<0,001	+
			Altura Media	0,881	n.s.
			Matorral FC	<0,001	+
			Matorral FS	0,035	+
			Cobertura Rocas	0,727	n.s.
	Mesoescala	0,031	Semillas dispersadas	0,315	n.s.
			Cobertura arbórea	0,028	+
			Altura Media	0,183	n.s.
			Matorral FC	0,481	n.s.
			Matorral FS	0,371	n.s.
			Cobertura Rocas	0,576	n.s.
	Microescala	0,012	Semillas dispersadas	0,569	n.s.
			Cobertura arbórea	0,927	n.s.
			Altura Media	0,991	n.s.
			Matorral FC	0,554	n.s.
			Matorral FS	0,642	n.s.
			Cobertura Rocas	0,397	n.s.

15.4. DISCUSIÓN

Nuestro estudio muestra diferencias específicas entre especies leñosas en la tasa de depredación post-dispersiva por roedores, siendo *Juniperus* más consumida que *Berberis*. Estudios previos sobre estas especies (García 2001, Rey *et al.* 2002, Kollmann *et al.* 1998) sugieren que la preferencia del depredador por una determinada especie puede estar determinada por la morfología y la composición química de la propia semilla. En nuestro caso, las diferencias inter-específicas no pueden explicarse en términos de tamaño de la semilla (Gómez 2004), ni de características estructurales relacionadas con el grado de protección mecánica (Blate *et al.* 1998, García *et al.* 2005a), por lo que pueden ser debidas a las diferencias en contenido lipídico (Kerley y Erasmus 1991) o a la presencia de sustancias tóxicas (las semillas de *Berberis* contienen alcaloides, Kollmann *et al.* 1998). Aunque de magnitud reducida, estas diferencias en tasa de depredación entre especies podrían conllevar diferencias en tasas de reclutamiento que contribuirían a la estructuración de la comunidad de matorral (Rey *et al.* 2002, García *et al.* 2005a, Matías *et al.* 2008).

Las diferencias en depredación entre especies han de ser interpretadas en términos de la estructura espacial de la depredación y la relación de la misma con las variables ambientales. En este sentido, los modelos espaciales generados por el ACPMV fueron capaces de predecir entre el 40 y el 50% de la variación espacial periódica de la depredación en ambas especies, dentro de la "ventana de observación" establecida por el grano (distancia mínima entre puntos de muestreo cercana a 4 m) y la extensión (distancia máxima cercana a 800 m) del transecto. El resto de varianza no explicada correspondería a un patrón espacial aleatorio de depredación (Borcard y Legendre 2002). Por otra parte, los modelos espaciales perdieron fuerza predictiva al descender en el gradiente de escalas, indicando una mayor aleatoriedad en la actividad de los depredadores de semillas conforme se considera una escala más fina. El análisis conjunto de los efectos de la abundancia de semillas y las variables fisionómicas del hábitat muestra que la mayoría de los factores ambientales actúan sobre la intensidad de depredación a la escala espacial más amplia, siendo pocos los que muestran su efecto a mesoescala o a microescala.

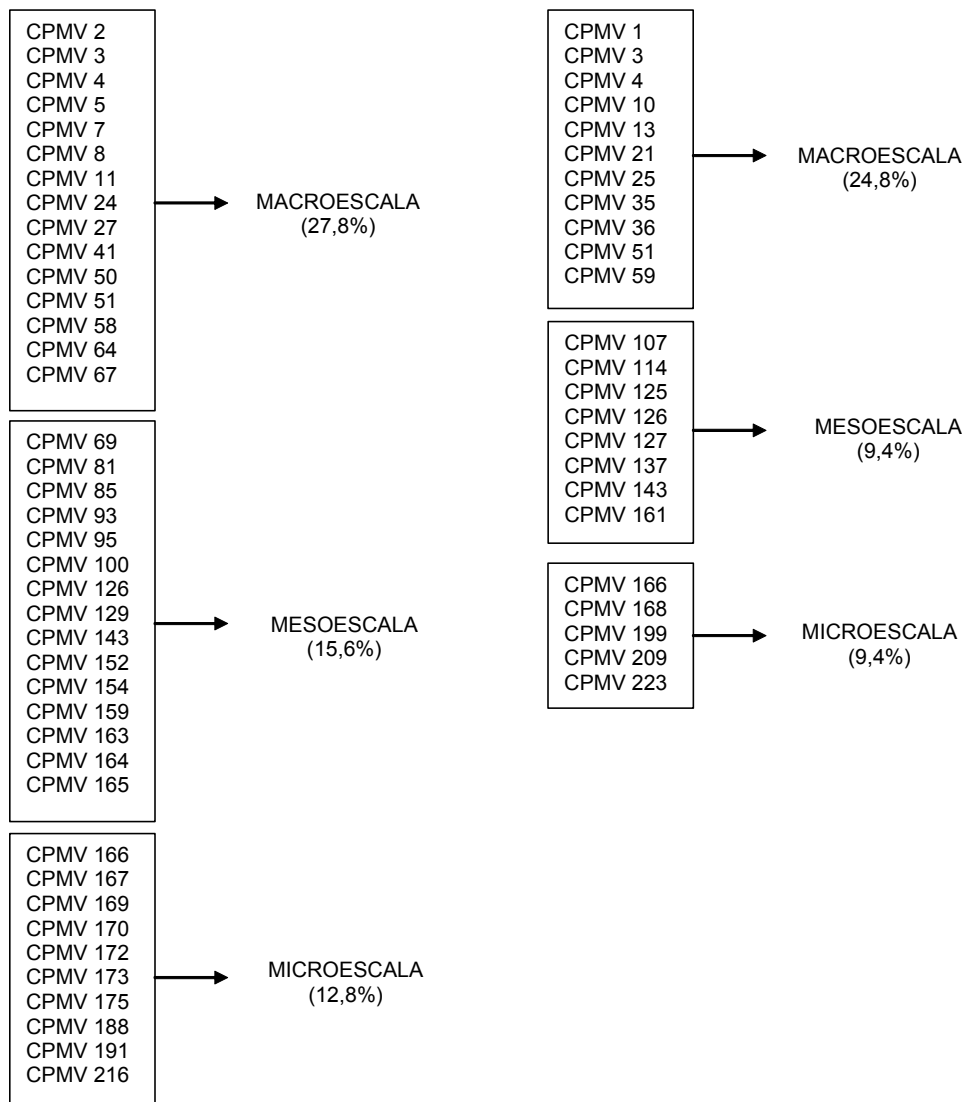


Figura 15.3. Vectores del ACPMV seleccionados como significativos en los modelos de regresión múltiple frente a las tasas de depredación de *Juniperus* y *Berberis*. Se muestran los vectores agrupados por escalas, indicándose el porcentaje de varianza espacial explicado por cada submodelo espacial (R^2 de regresión múltiple).

La abundancia de semillas dispersadas mostró efectos significativos sobre *Berberis* a macroescala, lo que sugiere existe un efecto denso-dependiente positivo del conjunto de semillas dispersadas, de forma que otras semillas más

palatables para los depredadores puedan atraer a éstos, incrementándose de este modo la depredación ocasional sobre *Berberis*. Sin embargo, el efecto de la densidad de semillas sobre *Juniperus* apareció a mesoescala y con un efecto contrario al ejercido sobre *Berberis*, reduciéndose la tasa de depredación conforme aumenta el número de semillas disponibles. Estos resultados corroboran los trabajos previos que evidencian la alta especificidad de los efectos denso-dependientes la necesidad de interpretar dichos efectos en relación a la palatabilidad de las semillas (Kwit *et al.* 2004, García *et al.* 2007).

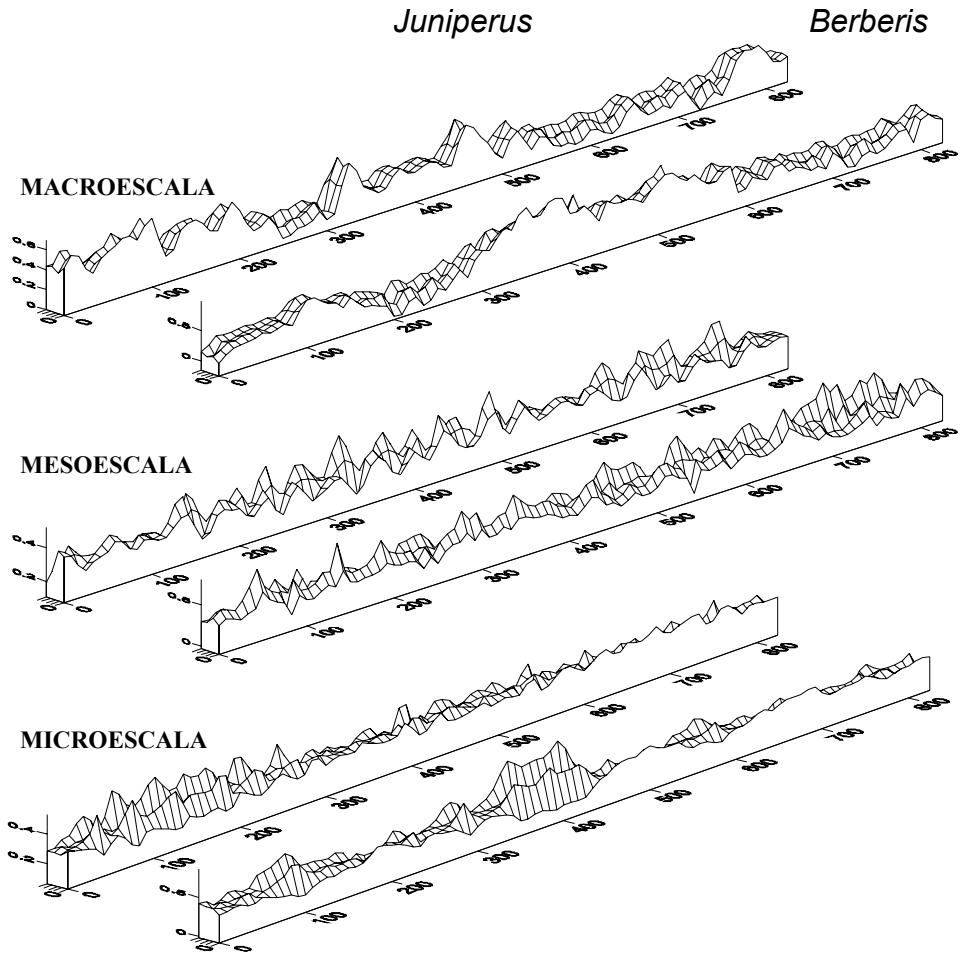


Figura 15.4. Representación de los valores las tasas de depredación de semillas de *Juniperus* y de *Berberis*, predichos por los submodelos espaciales a distintas escalas (macro-, meso- y microescala) generados por los vectores de coordenadas principales de matrices de vecinos, para los distintos puntos de muestreo a lo largo del transecto.

La cobertura arbórea fue el único factor fisionómico que afectó del mismo modo a la depredación de las dos especies estudiadas. Esta relación probablemente se deba al aumento de densidad de ratones en las zonas forestales respecto a las zonas abiertas o de matorral (Rey *et al.* 2002, García *et al.* 2005a). Las diferencias en densidad de depredadores entre hábitats generarían un gradiente de probabilidad de depredación suficientemente amplio como para generar diferencias espaciales generalizables entre distintas especies de semillas. Por otra parte, la cobertura de matorral, tanto de fruto carnoso como de fruto seco, mostró efectos positivos sólo sobre *Berberis* y a macroescala. Finalmente, el único factor que mostró efectos a microescala fue la cobertura de rocas sobre la depredación de *Juniperus*, aunque también mostró un efecto significativo y del mismo signo a la escala espacial más amplia. Tanto el efecto positivo de la cobertura y la altura del matorral, como el efecto negativo de la cobertura rocosa se explicarían por una selección de los roedores hacia los microhábitats que les ofrecen mayor protección frente a los depredadores, como se ha demostrado en otros ecosistemas mediterráneos (Schupp y Fuentes 1995, Rey *et al.* 2002, García 2001, Matías *et al.* 2008).

La mayoría de los efectos evidenciados de los factores ambientales sobre la depredación de semillas fueron escala-dependientes, y sólo el papel de la cobertura rocosa puede considerarse como un caso de consistencia entre escalas se mantuvo similar a lo largo del abanico de escalas considerado, apareciendo tanto a macro- como a microescala con una tendencia negativa de intensidad similar (García y Obeso 2003, Herrera y García en este volumen).

En términos generales, este trabajo pone de manifiesto cómo los patrones espaciales de supervivencia de distintas especies de semillas dentro de la misma comunidad vegetal son el resultado de una compleja interacción entre características intrínsecas y ambientales que actúan de forma idiosincrásica dependiendo de la especie y de la escala espacial. Proponemos que esta complejidad mediada por las diferencias de escala sea tenida en cuenta a la hora de explicar la coexistencia de especies de matorral en estos sistemas de alta montaña (Kneitel y Chase 2004).

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