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

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ECESPA
AEET
Servicio de Publicaciones
Dykinson, S.L.
CEMACAM Font Roja-Alcoi CENTRO EDUCATIVO DEL MEDIO AMBIENTE Alcoi - Alicante
CAM Caja Mediterráneo OBRAS SOCIALES

Editorial DYKINSON, S.L.
Meléndez Valdés, 61 - 28015 Madrid
Teléfono (+34) 91544 28 46 - (+34) 91544 28 69
e-mail: info@dykinson.com
http://www.dykinson.es http://www.dykinson.com

ISBN: 978-84-9849-308-5
Depósito Legal:

Preimpresión:

Besing Servicios Gráficos, S.L.
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¿Es posible distinguir los patrones acumulativos en los cambios de escala? Un caso práctico con interacciones planta-frugívoro

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RESUMEN

Los estudios de escalamiento son esenciales para establecer vínculos entre patrones, procesos y mecanismos ecológicos. Ciertos patrones pueden mantener su forma a lo largo de un rango de escalas, generando un dominio de escala o una situación de concordancia espacial. Dicha concordancia puede deberse a que los patrones controlados por mecanismos que operan en las escalas inferiores se acumulan a lo largo del gradiente de escalas. Para evaluar la importancia de la acumulación de patrones entre escalas, analizamos la relación entre el frugivorismo por aves sobre árboles individuales de *Crataegus monogyna* y la disponibilidad de frutos carnosos. Tomando como puntos de muestreo la posición de 12 árboles focales, consideramos dos escalas espaciales, el entorno inmediato del individuo (radio 10 m) y el entorno paisajístico del mismo (radio 50 m). La intensidad de frugivorismo se relacionó positivamente con la disponibilidad de frutos a la escala fina, considerando el

frugivorismo de los árboles focales con la abundancia de frutos en su entorno inmediato, y a escala amplia, relacionando el frugivorismo promedio entre árboles con la disponibilidad de frutos en el entorno paisajístico. Sin embargo, cuando evaluamos la relación entre frugivorismo individual y disponibilidad de frutos en el entorno paisajístico, eliminando el tamaño de cosecha de los árboles focales, el patrón positivo desapareció. Esto indica que el ajuste entre frugivorismo y abundancia de frutos a escala amplia no se produce por un rastreo de las aves a escala paisajística, sino por el efecto acumulado del rastreo, a escala fina, de las cosechas individuales. El cambio de juego de grano muestral permitió evaluar la aparición de un patrón a escala amplia eliminando el peso de la variación a escala fina, posibilitando la identificación de patrones acumulados a lo largo del gradiente de escalas.

16.1. INTRODUCCIÓN

La determinación de la escala espacial característica de los patrones ecológicos, o escala-dependencia, mejora nuestra capacidad para establecer relaciones entre las respuestas biológicas de los organismos y las condiciones ambientales (Wiens 1989; Levin 1992; Borcard *et al*. 2004), así como para explicar la coexistencia entre organismos que compiten por los mismos recursos (Inouye 1999; Westphal *et al*. 2006).

El fenómeno de escala-dependencia puede definirse también mediante el término de *discordancia entre escalas*, refiriéndose éste a la desaparición o cambio de signo en un patrón ecológico cuando se practica un cambio de escala (Allen y Hoekstra 1991; García y Ortiz-Pulido 2004; Capítulo 2; Fig. 16.1). Sin embargo, es posible que el patrón generado por un determinado mecanismo físico o biológico deje de ser fiel a una escala espacial concreta y permanezca constante a lo largo de la totalidad o una parte importante del rango de las escalas objeto de estudio, dando lugar a una situación de *concordancia entre escalas* y originando los denominados *dominios de escala* (Wiens 1989; Capítulo 2). Por ejemplo, en un estudio de ajuste espacial consumidor-recurso realizado con aves frugívoras y frutos de olivo (*Olea europaea* var. *europaea*) en el valle del Guadalquivir, Rey (1995) encontró un patrón de respuesta positiva de la abundancia de aves a la disponibilidad de frutos, que fue concordante a lo largo tres escalas espaciales consecutivas: escala de parche (extensión muestral de centenas de metros cuadrados), escala local ($\sim$ 6-9 km^2) y escala regional ($\sim$ 10.000 km^2). Estos resultados pueden indicar que las aves presentan una sucesión jerárquica de respues-

tas comportamentales (Sallabanks 1993), seleccionando primero entre regiones, luego localidades y por último entre parches con mayor disponibilidad de frutos. En otras palabras, un mismo proceso ecológico (rastreo de recursos) generaría un patrón consistente en un dominio de escala mediante distintos mecanismos (criterios comportamentales de decisión por las aves, con diferentes patrones de movimiento y desplazamiento) a distintas escalas (ver también Schaefer y Messier 1995).

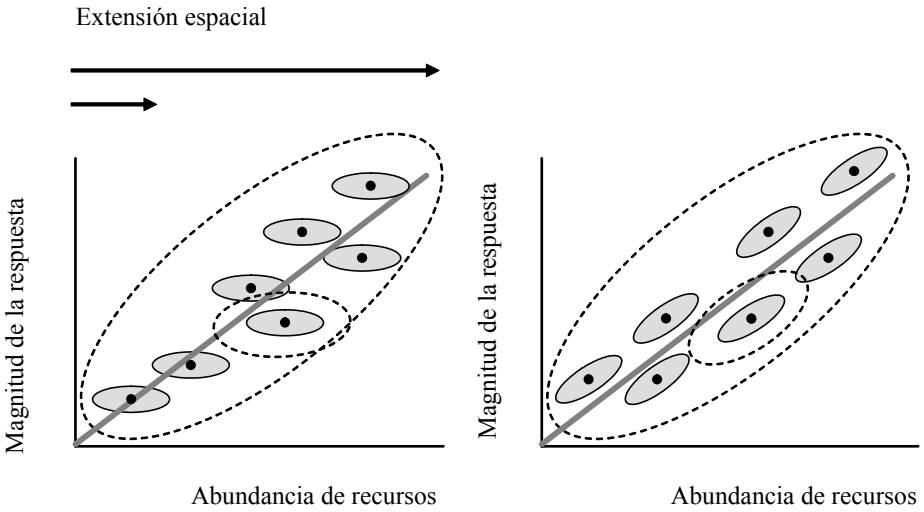

Figura 16.1. *Representación hipotética de un patrón ecológico (respuesta biológica de un consumidor frente a la abundancia de recursos) a lo largo de un gradiente de escalas (extensión espacial) mostrando los fenómenos de a) discordancia y b) concordancia entre escalas espaciales (modificado de García y Ortiz-Pulido 2004). Las elipses grises representan las nubes de correlación de puntos entre los parámetros que componen el patrón a escala fina, en distintos sectores de la extensión espacial amplia. Los puntos negros centrales son los valores promedio de cada sector a escala fina, y su combinación genera la nube de correlación entre los parámetros que componen el patrón a escala amplia. Obsérvese cómo en a) aparece un patrón positivo a escala amplia a pesar de no existir un patrón a la escala fina, mientras que en b) se representa un caso donde el patrón positivo en las escalas superiores es parcialmente debido a la acumulación de patrones que emergen a escalas inferiores.*

La interpretación de mecanismos escala-dependientes a partir de situaciones de concordancia de patrones en gradientes de escala ha de ser cautelosa, ante la posibilidad de que los patrones que observemos a escalas amplias se deban a patrones que se están generando en las escalas inmediatamente inferiores, pero que por un efecto acumulativo derivado del proceso analítico

se expresen también en las escalas superiores (Wu y Loucks 1995; Fauchald *et al*. 2000; Fauchald y Erikstad 2002; García y Ortiz-Pulido 2004; Fig. 16.1). Este efecto acumulativo es más probable cuando la varianza espacial de los parámetros biológicos que conforman el patrón en las escalas inferiores es grande, en comparación con la varianza en las escalas superiores (García y Ortiz-Pulido 2004). Retomando el ejemplo de Rey (1995), podemos plantear que si las aves eran capaces de acumular su actividad en parches con abundantes frutos, y las diferencias entre parches en abundancia de frutos eran muy marcadas, podría esperarse encontrar más aves en aquellos sectores regionales con mayor cobertura de parches con muchos frutos, sin necesidad de rastreo de recursos a escala de paisaje y gracias exclusivamente al rastreo a escala fina. En dicho caso, un mecanismo operativo a escala fina estaría contribuyendo decisivamente a generar un patrón a una escala superior.

El objetivo del presente trabajo es llamar la atención sobre el fenómeno de acumulación de patrones en los cambios de escala. Para la identificación de dichos patrones acumulativos, proponemos una aproximación metodológica basada en un juego de cambio de grano muestral, de forma que pueda evidenciarse el peso de la varianza a escala fina en la aparición de patrones a escala amplia.

16.2. MATERIAL Y MÉTODOS

El patrón ecológico analizado a distintas escalas fue, como en el ejemplo anterior, el ajuste entre la abundancia de frutos carnosos de una planta leñosa y la magnitud de interacción de las plantas productoras con las aves frugívoras. Como sistema biológico de estudio utilizamos la interacción entre el espino albar (*Crataegus monogyna* Jacq.), un árbol de pequeño porte (10 m) típico de matorrales y bosques secundarios europeos y las aves del género *Turdus* spp. (mirlos y zorzales). Estas aves consumen los frutos enteros y posteriormente defecan las semillas intactas actuando como dispersantes legítimos (Snow y Snow 1988; García *et al*. 2005b). El estudio se realizó en la Sierra de Peña Mayor-Trigueiro, un macizo montañoso de altitud media de la cordillera Cantábrica (Asturias, España). La especie de estudio aparece, junto con otras especies leñosas ornitócoras como *Ilex aquifolium*, *Taxus baccata*, *Sorbus aucuparia* y *S. aria,* formando parte de rodales de bosque secundario de tamaño variable, embebidos en una ma-

triz de pastizal-brezal de uso ganadero. En esta localidad, los frutos de *C. monogyna* maduran en verano y son consumidos por las aves entre septiembre y febrero, principalmente por el mirlo *Turdus merula*, el zorzal alirrojo *T. iliacus*, el zorzal real *T. pilaris* y el zorzal charlo *T. viscivorus*. El estudio se desarrolló durante el otoño-invierno de 2005/2006, un año en el cual *C. monogyna* fue prácticamente la única especie que produjo cosechas importantes de frutos carnosos en los bosques estudiados.

El muestreo comprendió 58 árboles distribuidos a lo largo de una superficie de unas 30 ha. En cada árbol se estimó la actividad frugívora de los zorzales dispersantes a lo largo del período de dispersión de semillas, así como su tamaño de cosecha y la disponibilidad de frutos maduros en todos los árboles de fruto carnoso en un área circular de radio 10 m alrededor de cada árbol focal (Fig. 16.2). La actividad de los frugívoros se midió como la proporción de frutos de *C. monogyna* manipulados por las aves y caídos bajo la copa, respecto al total de frutos caídos, y encontrados en 3 cuadrados permanentes de 50 x 50 cm situados bajo el dosel de las plantas individuales (ver también García y Chacoff 2007). Los frutos manipulados, resultado de fallos de manejo por parte de las aves cuando se alimentan, son fácilmente reconocibles, gracias a las marcas de pico en forma de V que quedan en su superficie. El tamaño de cosecha de cada árbol se estimó multiplicando el número promedio de frutos contados en 10 ramas escogidas al azar por el número total de ramas con frutos en el dosel del árbol. La disponibilidad de frutos en el entorno de 10 m de radio se calculó sumando a la cosecha del árbol focal las cosechas acumuladas de todos los árboles en fruto de distintas especies en dicha superficie (excluyendo individuos de altura $\leq$1.5 m y dbh $\leq$4 cm). Dichas cosechas se estimaron visualmente, mediante una escala semi-logarítmica (0,1: $\leq$10 frutos; 2: $\leq$100; 3: $\leq$1,000; 4: $\leq$10,000; 5 $>$ 10,000). Todas las disponibilidades acumuladas se expresaron finalmente en escala logarítmica ($\log_{10}$).

Para realizar el análisis pluriescalar focalizamos el muestreo en 12 de estos árboles y calculamos para ellos la disponibilidad de frutos en un área circular de 50 m de radio a su alrededor, sumando las disponibilidades de frutos de todos los árboles focales y de sus respectivos entornos de 10 m de radio comprendidos en cada uno de esos entornos de 50 m (Fig. 16.3). El número de árboles incluidos en cada uno de estos entornos de 50 m de radio no fue aleatorio, sino que aspiró a incluir al menos 2-3 árboles focales alrededor de cada uno de los 12 árboles seleccionados con el fin de repre-

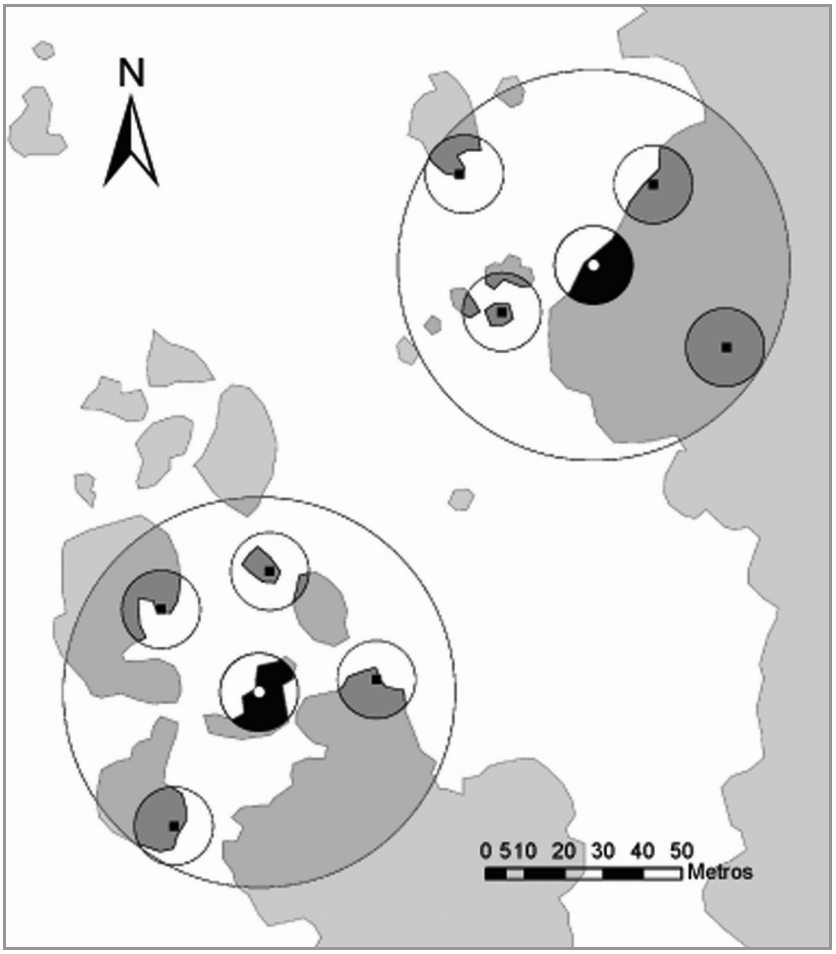

Figura 16.2. *Representación del diseño muestral obtenido mediante un Sistema de Información Geográfica (GIS) para relacionar la magnitud de frugivorismo con la disponibilidad de frutos a distintas escalas espaciales. Los círculos representan los árboles focales mientras que los cuadrados representan los árboles incluidos en los sectores de 50 m de radio (ver texto). Se representa la cobertura forestal digitalizada para corregir su efecto sobre la disponibilidad de frutos en la escala de 10 m (área roja) y 50 m (área ocre). Una versión en color de esta figura se encuentra en el CD adjunto (carpeta "Capítulo 16", archivo "Figura 16.2.jpg").*

sentar los parámetros de estudio con un tamaño de muestra suficientemente representativo. Este procedimiento tuvo el inconveniente de sobrevalorar la disponibilidad de frutos en aquellos sectores del paisaje de baja cobertura forestal. Para corregir este efecto, calculamos la disponibilidad de frutos a escala amplia mediante el producto de la disponibilidad de fru-

tos estimada en los entornos de 50 m de radio por el porcentaje de cobertura forestal (calculado mediante un Sistema de Información Geográfica y ortofotos escala 1:5000 donde los árboles fueron geoposicionados y la cobertura forestal digitalizada). Finalmente, este procedimiento de ampliación de la escala de observación a partir de los árboles focales nos permitió establecer 12 sectores de paisaje espacialmente independientes (no solapados).

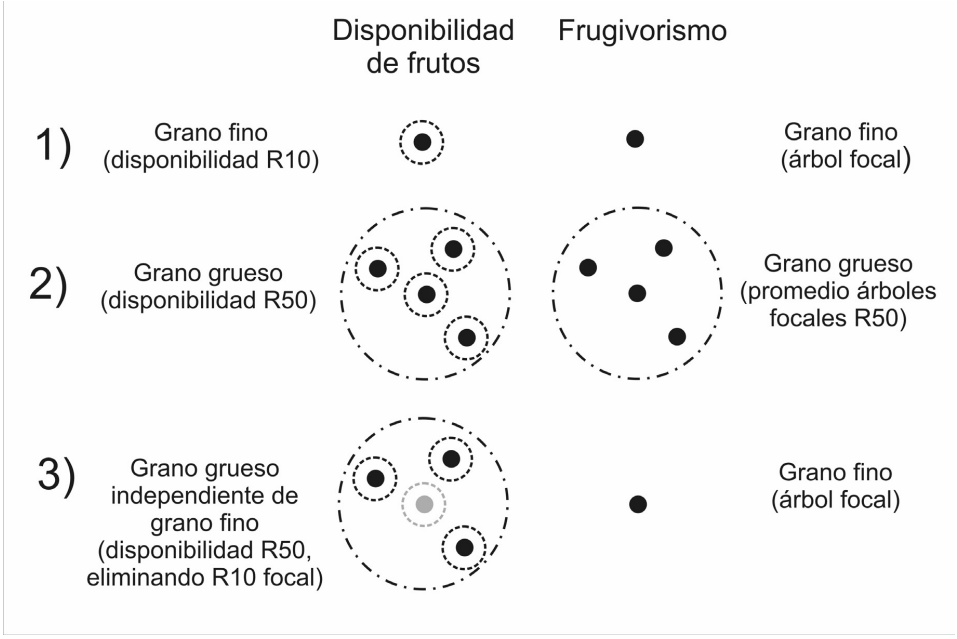

Figura 16.3. *Combinaciones de tamaño de grano en la relación entre la disponibilidad de frutos y la magnitud de frugivorismo en* Crataegus monogyna*, para el análisis pluriescalar y la detección de un patrón acumulativo a lo largo del gradiente de escala. El análisis a escala fina se realizó considerando un grano fino en ambas variables (1). El análisis a escala amplia se realizó ampliando el tamaño de grano en ambas variables (2). La detección del patrón acumulativo en el cambio de escala se realizó combinando un grano fino en la variable respuesta y un grano grueso, independiente de la variación de grano fino, en la variable predictora (3).*

16.3. ANÁLISIS DE DATOS

La detección de la aparición de un patrón acumulativo en el cambio de escala se basó en el contraste entre el resultado del análisis pluriescalar y el re-

sultado de una combinación de juegos de tamaño de grano que intentara limitar el peso de la variación a escala fina en el patrón a escala amplia. El análisis pluriescalar se basó en la verificación de un mismo patrón sobre dos escalas diferenciadas por un cambio en el tamaño de grano y en la extensión espacial de la realidad muestral (Allen y Hoekstra 1991; Capítulo 2; Fig. 16.3). La verificación a escala fina se basó en relacionar, mediante un análisis de regresión simple, la magnitud de frugivorismo (variable dependiente) de los 12 árboles focales seleccionados con la disponibilidad de frutos en el entorno de 10 m de radio a su alrededor (variable independiente, Fig. 16.3). Una relación positiva y significativa entre ambas variables se interpretaría como un rastreo de recursos a escala de la planta individual, determinado en gran medida por su propio tamaño de cosecha. La verificación a escala amplia se realizó relacionando, con un test similar, la magnitud de frugivorismo promedio de los 12 sectores paisajísticos establecidos en el entorno de radio 50 m alrededor de los árboles focales con la disponibilidad corregida de frutos en dichos sectores (Fig. 16.3). Una relación positiva y significativa entre ambas variables podría interpretarse como un rastreo de recursos a escala de paisaje, determinado por la abundancia global de frutos en los rodales forestales, pero también como un patrón acumulativo debido a los efectos de rastreo sobre las cosechas de los árboles individuales. Para diferenciar entre estas dos posibilidades, se verificó la relación frugivorismo-abundancia de frutos, combinándose un tamaño de grano fino en la variable dependiente (magnitud de frugivorismo de la planta focal, N=12) con un tamaño de grano grueso, pero independiente del efecto de grano fino, en la variable independiente (disponibilidad acumulada corregida de frutos en el entorno de radio 50 m alrededor de los árboles focales, sin tener en cuenta la abundancia de frutos en la planta focal y su entorno de 10 m de radio; Fig. 16.3). Una relación positiva y significativa entre ambas variables indicaría que la magnitud de frugivorismo sobre las plantas focales depende de la abundancia de frutos en su contexto paisajístico, independientemente del efecto de su propio tamaño de cosecha y que, por tanto, el patrón a escala amplia no se debe a un efecto acumulativo sino a un mecanismo idiosincrásico de dicha escala.

16.4. RESULTADOS Y DISCUSIÓN

La magnitud de frugivorismo soportada por los árboles focales se relacionó positivamente con la disponibilidad frutos en el entorno de 10 m de

radio ($R^2 = 0.60$, $F = 14.91$, $p < 0.001$, N=12; Fig 16.4a). Debido a la baja producción de frutos de otras especies productoras de fruto carnoso en el año en que se llevó a cabo el estudio, puede interpretarse que esta relación se debió principalmente al efecto del tamaño de cosecha de los propios árboles focales, implicando un rastreo a escala espacial fina por parte de los frugívoros. Este resultado coincide con estudios previos que señalan el papel de la disponibilidad de frutos sobre la propia planta como factor principal de éxito de dispersión, y que se explica en virtud de una mayor eficacia de aprovisionamiento de los frugívoros en aquellas plantas individuales con más frutos (Davidar y Morton 1986; Sallabanks 1992). De forma similar, la magnitud promedio de frugivorismo soportado por los árboles que se encontraban en los sectores paisajísticos de 50 m de radio, se relacionó positiva y significativamente con la disponibilidad acumulada de frutos en dichos sectores ($R^2 = 0.51$, $F = 10.47$, $p < 0.001$, N=12; Fig. 16.4b). En base a estos resultados, podría afirmarse que las aves frugívoras realizan un rastreo de los recursos a escala amplia, seleccionando sectores dentro del paisaje donde la disponibilidad acumulada de frutos es mayor. Este comportamiento ya ha sido evidenciado en otras aves frugívoras de la familia Muscicapidae (*Sylvia* spp. y *Turdus* spp., p.ej. Rey 1995, García y Ortiz-Pulido 2004; Tellería y Pérez-Tris 2007) y parece potenciado por la capacidad de estas aves de realizar vuelos nomádicos y desplazamientos en bando a cierta altura por encima del dosel forestal (Santos 1985). Como planteamos en la Introducción, la concordancia entre escalas en términos de rastreo de recursos podría explicarse como una cadena jerárquica de respuestas comportamentales por parte de los frugívoros, decidiendo, en primer término, aprovisionarse en aquellos sectores de paisaje con más frutos, y, en segundo término, una vez dentro de esos sectores, seleccionando los árboles con mayores tamaños de cosecha o con más frutos en su entorno inmediato (ver Sallabanks 1993 para cadena de respuestas a escala aún más fina).

¿Consistencia o acumulación de patrones entre escalas espaciales?

A pesar de la fuerte correlación positiva entre frugivorismo y abundancia de frutos en las dos escalas espaciales analizadas, no podemos atribuir explícitamente la aparición del patrón positivo en la escala superior a un mecanismo que opera a escala paisajística. De hecho, la magnitud de

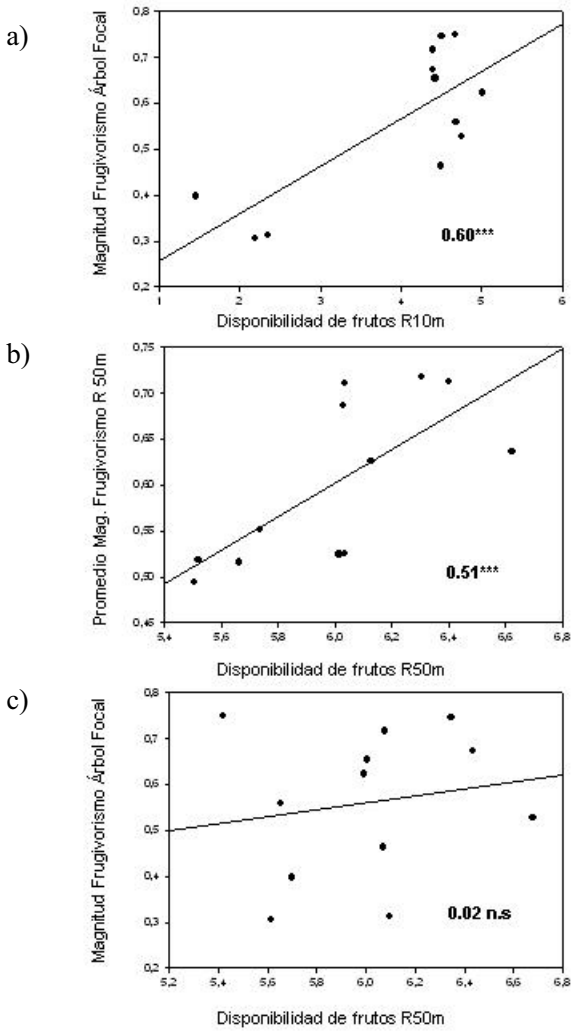

Figura 16.4. *a) Relación lineal entre la magnitud de frugivorismo y disponibilidad de frutos a escala fina (10 m de radio alrededor de los árboles focales). b) Valores promedio de la magnitud de frugivoría calculada a partir de los árboles incluidos en sectores circulares de 50 m de radio, en relación con la disponibilidad de frutos en esa escala. c) Relación entre la magnitud de frugivorismo en árboles focales y la abundancia de frutos a escala amplia (excluyendo el tamaño de cosecha del árbol focal). Se indica el coeficiente de determinación (R^2) y el grado de significación de cada ajuste de regresión (n.s.: $P > 0.05$, ***: $P < 0.001$).*

frugivorismo de los árboles focales individuales fue independiente de la disponibilidad de frutos presentes en el entorno de 50 m de radio alrededor de dichos árboles, eliminando la cosecha y la disponibilidad en el entorno inmediato del propio árbol focal ($R^2 = 0.02$, $F = 0.86$, $p > 0.05$, Fig.16.4c). Esto indica que la magnitud de interacción que soportó un árbol individual fue en gran medida independiente de la disponibilidad de recurso a escala de paisaje, y que el contexto a escala amplia apenas si condicionó las respuestas individuales de los organismos interactores (pero ver García *et al*. 2001). Por tanto, el dominio de escala observado para las dos escalas de estudio parece consecuencia más de mecanismos que operan en la escala inferior, como la respuesta de las aves a los tamaños de cosecha de las plantas individuales, que de una cadena jerárquica de respuestas de rastreo en el paisaje y dentro de los rodales.

La aparición de un patrón acumulativo en este sistema parece venir facilitada por dos aspectos. En primer lugar, y tal y como se especificó antes, el muestreo se realizó en un año con muy baja disponibilidad de frutos de especies alternativas, donde los frutos de *C. monogyna* eran prácticamente el único recurso para los frugívoros. El paisaje estuvo, por tanto, caracterizado por una fuerte heterogeneidad a escala fina, muy determinada por las diferencias en tamaño de cosecha entre árboles individuales potencialmente cercanos, pero una menor heterogeneidad a escala amplia, ya que las plantas con frutos se distribuyen a lo largo del paisaje de estudio de forma más aleatoria que los frutos sobre los árboles individuales. Esta heterogeneidad también dependiente de la escala influyó probablemente en los frugívoros, determinando una mayor sensibilidad hacia las características de los árboles individuales y su entorno inmediato que hacia el paisaje a escala amplia. En segundo lugar, la alta conectividad estructural del sistema favorecería también el patrón acumulativo. En este sentido, la escasa separación entre rodales forestales y la presencia de árboles con frutos aislados en la matriz no forestal, que actuarían como "piedras de paso" (*stepping stones*, Guevara y Laborde 1993; Manning *et al*. 2006) entre rodales forestales favorecería el rastreo secuencial de los árboles de grandes cosechas por parte de las aves frugívoras y el efecto final de concentración de frugívoros en sectores paisajísticos con más árboles con abundante fruto.

Nuestros resultados sugieren que no existe una única escala que acapare la estrategia de rastreo de frutos por las aves, sino más bien un conjunto

de escalas que pueden evidenciar la importancia de distintos mecanismos de rastreo. La identificación y desglose de los dominios de escala es vital para comprender los procesos ecológicos en su conjunto, y para discernir los verdaderos mecanismos que están actuando en cada una de las escalas espaciales. Sin embargo, teniendo en cuenta que muchos de los estudios de escalamiento son observacionales y correlacionales, es necesario considerar también que los patrones pueden derivarse de la actuación de otros factores que también pueden ser escala-dependientes. Por ejemplo, en nuestro caso es posible que la magnitud de frugivorismo responda no sólo a la disponibilidad de frutos sino también a factores estructurales como la disponibilidad de perchas que las aves utilizan para posarse o de la propia cobertura forestal global (p. ej. García *et al*. 2001; García y Chacoff 2007).

Este estudio alerta sobre algunos de los problemas metodológicos y analíticos en los estudios de escalamiento, especialmente en sistemas cuya heterogeneidad sigue una estructura anidada y jerárquica, como las interacciones planta-animal (Kotliar y Wiens 1990). Puesto que diferentes mecanismos actúan a diferentes escalas (Levin 1992), es necesario observar los patrones a través de múltiples escalas espaciales y, además, llevar a cabo un correcto desglose de la varianza espacial que permita identificar el peso acumulativo de aquellos niveles donde se generan realmente los patrones (Kotliar y Wiens 1990; Jelinski y Wu 1996).

AGRADECIMIENTOS

Susana García y Alicia Valdés ayudaron enormemente en el trabajo de campo y laboratorio. Este trabajo se ha financiado con el proyecto CGL2004-2936/BOS (Ministerio Español de Educación y Ciencia) a DG, una beca de FPI (MEC) a JMH y un contrato del Programa Ramón y Cajal (MEC-Fondo Social Europeo) a DG.

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