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Birds as Suppliers of Seed Dispersal in Temperate Ecosystems: Conservation Guidelines from Real-World Landscapes

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Abstract: *Seed dispersal by animals is considered a pivotal ecosystem function that drives plant-community dynamics in natural habitats and vegetation recovery in human-altered landscapes. Nevertheless, there is a lack of suitable ecological knowledge to develop basic conservation and management guidelines for this ecosystem service. Essential questions, such as how well the abundance of frugivorous animals predicts seeding function in different ecosystems and how anthropogenic landscape heterogeneity conditions the role of dispersers, remain poorly answered. In three temperate ecosystems, we studied seed dispersal by frugivorous birds in landscape mosaics shaped by human disturbance. By applying a standardized design across systems, we related the frequency of occurrence of bird-dispersed seeds throughout the landscape to the abundance of birds, the habitat features, and the abundance of fleshy fruits. Abundance of frugivorous birds in itself predicted the occurrence of dispersed seeds throughout the landscape in all ecosystems studied. Even those landscape patches impoverished due to anthropogenic disturbance received some dispersed seeds when visited intensively by birds. Nonetheless, human-caused landscape degradation largely affected seed-deposition patterns by decreasing cover of woody vegetation or availability of fruit resources that attracted birds and promoted seed dispersal. The relative role of woody cover and fruit availability in seed dispersal by birds differed among ecosystems. Our results suggest that to manage seed dispersal for temperate ecosystem preservation or restoration one should consider abundance of frugivorous birds as a surrogate of landscape-scale seed dispersal and an indicator of patch quality for the dispersal function; woody cover and fruit resource availability as key landscape features that drive seedfall patterns; and birds as mobile links that connect landscape patches of different degrees of degradation and habitat quality via seed deposition.*

Keywords: anthropogenic landscapes, Cantabrian forest, ecosystem services, fleshy-fruited plants, frugivorous birds, Mediterranean shrubland, mobile links, Patagonian forest, seed dispersal

Aves como Proveedoras de Dispersión de Semillas en Ecosistemas Templados: Directrices de Conservación desde Paisajes del Mundo Real

Resumen: *La dispersión de semillas por animales se considera como una function ecosistémica crucial, que controla las dinámicas de las comunidades de plantas en los hábitats naturales y la recuperación de la vegetación en los paisajes alterados por el hombre. Sin embargo, existe una carencia de conocimiento ecológico adecuado para desarrollar directrices básicas de conservación y gestión de este servicio ecosistémico. Cuestiones esenciales, tales como hasta qué punto la abundancia de animales frugívoros sirve para predecir la función de dispersión de semillas, o si la heterogeneidad paisajística antropogénica condiciona el papel de los dispersantes, permanecen sin respuesta. Estudiamos, en tres ecosistemas templados, la dispersión de semillas*

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por aves frugívoras en mosaicos paisajísticos moldeados por las perturbaciones antrópicas. Mediante la aplicación de un diseño estandarizado en todos los sistemas, relacionamos la frecuencia de aparición de semillas dispersadas por aves a lo largo del paisaje con la abundancia de aves, los rasgos del hábitat y la abundancia de frutos carnosos. La abundancia de aves frugívoras predijo, por sí misma, la aparición de semillas dispersadas a lo largo del paisaje en todos los ecosistemas estudiados. Incluso aquellos rodales paisajísticos empobrecidos por perturbaciones antrópicas recibieron algunas semillas dispersadas tras ser visitados intensamente por las aves. No obstante, la degradación antropogénica del paisaje afectó ampliamente a los patrones de deposición de semillas, reduciendo la cobertura de vegetación leñosa y la disponibilidad de recursos frutales que atraían a las aves y fomentaban la dispersión de semillas. El papel relativo de la cobertura leñosa y la disponibilidad de frutos en la dispersión de semillas por aves difirió entre ecosistemas. Nuestros resultados sugieren que, para gestionar la dispersión de semillas de cara a conservar o restaurar los ecosistemas templados, se debe considerar la abun dancia de aves frugívoras como un parámetro representante de la dispersión de semillas a escala de paisaje y un indicador de la calidad del rodal para la function de dispersión, la cobertura leñosa y la disponibilidad de recurso frutal como rasgos paisajísticos clave que controlan los patrones de deposición de semillas, y a las aves como vínculos móviles que conectan, a través de la deposición de semillas, rodales de paisaje con diferentes grados de degradación y calidad de hábitat. .

Palabras Clave: aves frugívoras, bosque cantábrico, bosque patagónico, dispersión de semillas, matorral mediterráneo, paisajes humanizados, plantas de fruto carnoso, servicios ecosistémicos, vínculos móviles

Introduction

Seed dispersal is a process that controls the long-term dynamics of plant communities and the recovery of vegetation in human-disturbed habitats (Howe & Miriti 2004). Because of the roles seed dispersal plays in supporting biodiversity, this ecological function can be considered an ecosystem service that contributes to human well-being through the regulation of ecosystem processes and the provision of natural resources (Kremen 2005). In many terrestrial tropical and temperate ecosystems, seed dispersal is carried out mostly by animal vectors with strong vagility, such as birds or bats that feed on seeds or fruits and drop them far from source plants (Jordano 2000). These animals are termed mobile agents, or mobile links, and they connect different habitat patches across the landscape via seed transfer (Lundberg & Moberg 2003; Kremen et al. 2007). This kind of large-scale connection is purported to contribute strongly to plant persistence in fragmented landscapes and to ecosystem resilience, especially when seed movement involves the transfer of seeds from mature habitats into degraded patches (Lundberg & Moberg 2003; Bengtsson et al. 2003).

As with other animal-related, trophic-based ecosystem services, such as pollination, there is a lack of ecological knowledge of seed dispersal that can be readily translated into conservation action (Kremen et al. 2007). In fact, essential questions, such as whether the abundance of frugivorous animals is an effective surrogate of seed-dispersal service across the landscape of different ecosystems, have been scarcely explored (Pejchar et al. 2008). Although seed delivery is the obvious consequence of frugivory, the link between frugivore activity and the magnitude of seed dispersal is far from axiomatic. For example, some landscape patches may receive disproportionate seeding after repeated use by small numbers of frugivores (e.g., sites used by male birds for territorial displays, Wenny & Levey 1998). More importantly, the movement of many frugivores across the landscape is usually constrained by habitat features, rendering the result of the frugivore-seed relationship more dependent on environmental correlates (e.g., habitat cover, predation risk) than on frugivore abundance per se (Carlo & Morales 2008; García et al. 2009). Thus, to develop strategies to preserve seed dispersal in real-world landscapes, it is essential to assess the role of frugivorous animals by considering the importance of environmental gradients on animal activity, especially when these gradients are the consequence of anthropogenic habitat degradation (e.g., Sanford et al. 2008). Frugivore response to land-use gradients, however, is idiosyncratic; some frugivores are sensitive to fragmentation and reluctant to use the matrix of degraded habitat (e.g., Cordeiro & Howe 2003; Kirika et al. 2008) or are affected by landscape-scale fruit shortages when there is no apparent change in habitat cover (Rey 1995; Tellería et al. 2005), whereas others are able to persist in highly modified landscapes (e.g., Sekercioglu et al. 2007; Gomes et al. 2008) and even disperse seeds into the degraded matrix (Pejchar et al. 2008; Herrera & García 2009).

We focused on the ecosystem function of seed dispersal provided by frugivorous birds, a crucial group of dispersers in temperate regions where other highly mobile frugivores, such as bats, primates, or large ground-dwelling mammals, are almost absent (Sekercioglu 2006; Whelan et al. 2008). In three temperate ecosystems from two hemispheres, we sampled landscape mosaics shaped by human disturbance that were chosen to represent continuous gradients of habitat and fruit-resource availability. By applying a standardized sampling design, we related the frequency of occurrence of bird-dispersed seeds throughout the landscape to, simultaneously, the abundance of birds, habitat features, and fruit supply. Our objectives were to ascertain whether the abundance of frugivorous birds can serve as a surrogate of the magnitude of seed dispersal, irrespective of site, habitat structure, or availability of fruit resources; to address how human-caused landscape heterogeneity affects the seed-dispersal service supplied by birds; and to propose basic guidelines to manage bird-generated seed dispersal for ecosystem preservation or restoration.

Methods

Study Systems and Sites

Our study covers three systems, the Cantabrian forest of northern Spain, the Mediterranean shrubland of southern Spain, and the Patagonian forest of southern Argentina. These systems host structurally similar plant-frugivore networks. Bird-dispersed plants accounted for a large portion of plant richness and cover within original habitat patches and occurred occasionally in degraded patches. Frugivore guilds were dominated by passerines that feed almost exclusively on fleshy fruits during the fruiting season, and disperse the intact seeds through regurgitation or defecation.

In the Cantabrian region we examined mid-elevation secondary forests (Asturias Province, northern Spain). These forests have a uniform tree canopy layer 5–15 m high and an almost negligible understory layer of scattered tree saplings, short (<0.5 m tall) heaths, and forest herbs. Forest stands occur as different-sized fragments (from isolated remnant trees to patches of several hectares) embedded in a deforested matrix of stony pastures and heathland. The study area was in the Sierra de Peña Mayor (43°17′N, 5°30′W, 900 m asl). Forest covered 25% of the site, and the remaining area was covered by pasture and heathland and used as cattle rangeland. Fleshy-fruited trees accounted for about 70% of total tree cover (Table 1). Fruits ripen in autumn and are consumed almost exclusively by thrushes (*Turdus* spp.; Martínez et al. 2008).

In the Mediterranean region sampling took place in high-elevation shrublands of the western Mediterranean Basin (Granada Province, southern Spain) that contained fleshy-fruited tall shrubs, dry-fruited thorny scrub, and prostrate brooms. The shrub layer was uniform in height (0.5–2 m) and was disrupted only by small forest stands or isolated trees (*Pinus sylvestris*) 5–15 m tall. The horizontal structure was variegated, with small shrub patches

Table 1. Biological description of the temperate plant-frugivore systems examined in the study of the role of birds as seed dispersers of fleshy-fruited plants.

Plant species	*Fruit traits*	*Fruiting season (peak ripeness)*	*Bird species**
Cantabrian forest			
Ilex aquifolium (Aquifoliaceae), *Crataegus monogyna* (Rosaceae), *Taxus baccata* (Taxaceae), *Sorbus* spp. (Rosaceae)	10–15 mm diameter, sugar-rich, reddish berries 1–4 seeds (5–9 mm)	September– February (October)	*Turdus merula* (R, OI, 100 g, Turdidae), *Turdus iliacus* (OM, 65 g), *Turdus philomelos* (R, OI, 75 g), *Turdus pilaris* (OM, 110 g), *Turdus viscivorus* (R, OI, 130 g)
Mediterranean shrubland			
Berberis hispanica (Berberidaceae), *Juniperus communis* (Cupressaceae), *Lonicera arborea* (Caprifoliaceae), *Amelanchier ovalis* (Rosaceae)	6–12 mm diameter, lipid-rich, blue-black berries; 1–4 seeds (3–7 mm)	September–February (November)	*Erithacus rubecula* (R, OI, 17 g, Turdidae), *Phoenicurus ochruros* (R, OI, 17 g, Turdidae); *Sylvia atricapilla* (R, OI, 17 g, Sylviidae), *Sylvia undata* (OM, 9 g), *T. merula* (R, OI), *Turdus torquatus* (OM, 120 g), *T. viscivorus* (R, OI)
Patagonian forest			
Aristotelia chilensis (Elaenocarpaceae), *Azara microphylla* (Flacourtiaceae), *Luma apiculata* (Myrtaceae), *Schinus patagonicus* (Anacardaceae), *Berberis* spp. (Berberidaceae), *Maytenus boaria* (Celastraceae)	5–11 mm diameter, lipid-rich, blue-black berries; 1–5 seeds (1–4 mm)	December–March (February)	*Elaenia albiceps* (OM, 16 g, Tyrannidae), *Turdus falcklandii* (R, 88 g)

**Migratory status (R, resident; OI, overwintering individuals; OM, overwintering migrant) and average body weight indicated.*

intermingled with bare ground and rocks. The study area was in the Sierra Nevada National Park (37°5′N, 3°28′W, 1900 m asl) and until recently had been heavily used for cattle grazing, pasture, and forestry. Fleshy-fruited shrubs accounted for about 70% of total shrub cover (Table 1). Fruits ripen in autumn and are mainly consumed by thrushes (Table 1; Mendoza et al. 2009).

In the Patagonian region sampling took place in mid-elevation mature forests of Río Negro Province (southern Argentina), which are typical examples of South American temperate forest, with *Nothofagus dombeyi* and *Austrocedrus chilensis* as canopy species. The understory had up to 15 woody species. The forest had two well-differentiated forest layers: tree canopy reaching up to 40 m high and understory reaching up to 7 m high. The forest also had canopy gaps generated by tree fall. Forest stands occurred as large fragments intermingled with human-generated pastures, crops, and urban areas. The study was conducted in the Llao-Llao Forest Reserve (41°8′S, 71°19′W, 800 m asl), which protects a well-preserved forest that had been logged and cleared before gaining reserve status. Fleshy-fruited treelets accounted for about 80% of understory cover (Table 1). Fruits ripen in summer through autumn and are mostly consumed by White-crested Elaenias (*Elaenia albiceps*) (Table 1; Amico & Aizen 2005).

Sampling Framework

We recorded habitat features, abundance of fruits, abundance of frugivorous birds, and the magnitude of seed dispersal across long-distance transects. A single transect, following a straight line, was placed arbitrarily at each study site, avoiding large elevational gradients (< 250 m) and aiming to represent the whole range of variability in the local landscape (Fig. 1). Transects were 2500 × 20 m and were subdivided into 100 contiguous 25 × 20 m plots. Due to logistical constraints, the transect in the Patagonian forest was 1500 × 20 m and had 75, 20 × 20 plots. We sampled during one fruiting year—October 2004–February 2005 in the Cantabrian forest, October 2005–February 2006 in the Mediterranean shrubland, and January–March 2005 in the Patagonian forest.

Habitat Features and Fruit Abundance

Each plot was divided into 10, 5 × 10 m subplots (eight in Patagonian forest) that covered the entire area (five at each side of the longitudinal axis of the transect, Fig. 1).

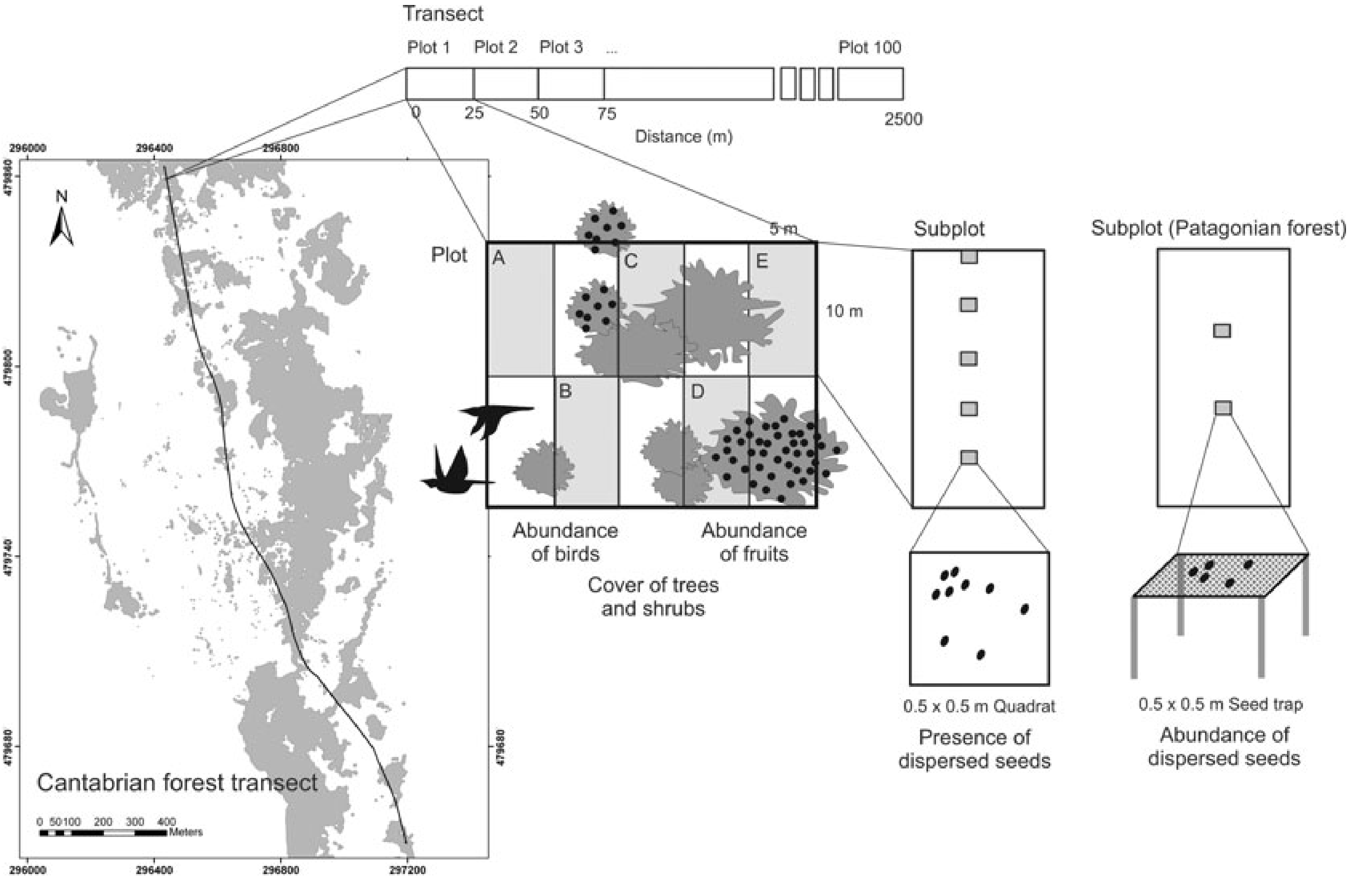

Figure 1. Framework for sampling bird abundance, habitat features, fruit abundance, and seed-dispersal magnitude (shaded, forest cover; unshaded, deforested matrix).

We sampled five (four in Patagonian forest) nonadjacent subplots per plot, sequentially alternating the left and right sides of the transect axis. In these subplots, we visually estimated the total cover (percentage) of tree canopy (woody plants $\geq$10 m tall) and understory (tree saplings, treelets, and tall shrubs $>$ 0.5 m and $<$ 10 m high).

We estimated the abundance of fleshy fruits in October in the Cantabrian forest and the Mediterranean shrubland and in January in the Patagonian forest. In these systems, fruiting is synchronous among individuals and species, and ripening occurs within 1–2 months (although fruits remain attached to trees for 1–3 additional months). Thus, we considered that a single sampling of fruit abundance at the beginning of the season provided an appropriate estimate of the spatial arrangement of fruit resources. In each subplot, we identified the plant species and assigned a size to the fruit crop (i.e., a value of fruit production by the individual tree) to each individual plant with at least 30% of its canopy area within the subplot (Fig. 1). Fruit crop size was estimated with a fruiting abundance index (FAI) with six semi-logarithmic categories: 0, without fruits; 1, 1–10 fruits; 2, 11–100; 3, 101–1,000; 4, 1,001–10,000; and 5, $>$10,000 (Saracco et al. 2004). The abundance of fruits per plot was the number of fruits per square meter. We calculated abundance by dividing the sum of FAIs (translated into interval-average values, except in the sixth interval, where we arbitrarily used a value of 25,000) from all subplots by the sampled surface.

Abundance of Frugivorous Birds

We sought to represent the use of different landscape patches by different quantities of birds over the whole fruiting season. Bird abundance at a given patch is difficult to estimate accurately over a short period of time because most of the bird species we studied are highly vagrant and mobile during the fruiting season. Thus, we distributed the sampling effort over the entire fruiting season, from the beginning of sampling. We performed bird censuses—one to three times a week during 2–3 months (15 censuses per site). For each census one watcher traveled the entire transect at a constant speed, between 08:00 and 12:00 on a clear day, and recorded the number of individuals of different frugivorous species seen or heard within a 25-m wide band on both sides of the transect axis. We estimated the abundance of frugivorous birds as the cumulative number of bird observations per plot for all censuses.

Seed Dispersal

Our goal was to evaluate the cumulative outcome of disperser activity for the whole fruiting season. For that we assessed the magnitude of seed dispersal late in the season in all systems. In the Cantabrian forest and the Mediterranean shrubland, sampling was performed in, respectively, early December and early January (i.e., 2–3 months after the beginning of the study). We recorded the presence of seeds dispersed by birds in five, 50 × 50 cm quadrats placed at 2-m intervals along each subplot (n = 2500 quadrats per site; Fig. 1). Seeds found in the remains of birds droppings were conspicuous. We estimated the magnitude of seed dispersal as the proportion of quadrats containing dispersed seeds ($n = 25$ quadrats/plot). We considered that, although some postdispersal seed loss probably did occur before the sampling, the method of seed monitoring in open-to-predators quadrats provided estimates of seed presence reliable enough for evaluation of the large-scale patterns of seed rain. In fact, seed removal by diurnal animals was never observed, and removal by nocturnal rodents is low during most of the dispersal season (predation frequency peaks late in winter, García et al. 2005*a*; Matías et al. 2009). In any case, those seeds showing signs of predation (open husks or teeth marks) found in the quadrats were considered dispersed seeds. Previous work in the same Cantabrian site demonstrated the suitability of seed monitoring in quadrats by comparing seed deposition in open-to-predators quadrats with seed deposition in paired seed traps that were unavailable to seed predators (García et al. 2005*b*). Also, in a random subsample of plots in the Mediterranean shrubland ($n = 32$), we deployed 10 seed traps (28 × 18 × 5 cm metal trays protected with a 1-cm pore wire mesh) per plot and found that the proportion of quadrats containing seeds was correlated with the average seed number per tray collected in February 2005 ($r = 0.473, p \leq 0.01, n = 32$).

In the Patagonian forest, due to low detectability of seeds once they were deposited on the forest floor (seeds were small, litter layer was dense, and there was little light at ground level), we discarded the method of seed monitoring in quadrats. Instead, at the beginning of the fruiting season, we established two seed traps, 2 m apart, at the center of each of the two central subplots of each plot (300 traps in total; Fig. 1). Each seed trap consisted of a square 0.5 × 0.5 m wire frame that supported a shallow, open-topped, 1-mm mesh nylon bag suspended 0.5 m above the ground on four wire poles. The contents of the traps were collected every week until late March 2005. We estimated the magnitude of seed dispersal as the average cumulative number of seeds of fleshy-fruited plants per trap per plot.

Statistical Analysis

We used structural equation modeling (SEM; Grace 2006) to analyze the relationship between bird abundance and seed dispersal, explicitly taking into account the role of habitat features and fruit abundance on frugivore activity. Structural equation models (e.g., path analysis) state a causal scheme, or path diagram, that represents a series of causal links derived from logical relationships within a group of variables and allows partitioning of correlation between variables into direct and indirect effects. Direct effects are represented by links between consecutive variables and are measured by regression coefficients.

We hypothesized that seed dispersal was affected by forest and understory cover, fruit abundance, and bird abundance, and interpreted these direct links as follows. (1) Variation in seed dispersal accounted for by forest or shrub cover represents disperser activity exclusively conditioned by habitat features (e.g., when, irrespective of their abundance, birds search for a protective canopy or perches for vigilance, resting, or foraging on nonfruit resources). (2) Variation in seed dispersal accounted for by fruit abundance represents disperser activity when tracking fruits (e.g., when birds spend more time in rich fruit patches). (3) Variation in seed dispersal accounted for by bird abundance alone represents disperser activity irrespective of the response to habitat features and the activity of tracking fruits.

The path model also took into account indirect effects, represented by the links between forest and shrub cover and fruit abundance (fruit availability may depend on the cover of fruit-bearing plants [i.e., tree canopy may overshadow the understory, hampering fruit production]); forest cover and shrub cover (tree canopy may outcompete shrubs); forest and shrub cover and bird abundance (birds may gather in patches with higher cover to search for protection or nonfruit resources); and fruit abundance and bird abundance (fruit resource tracking may affect the entire bird population). This causal scheme was tested for each study system. We removed nonsignificant paths from the saturated models sequentially, until the best-fit model determined by the Akaike's Information Criterion (AIC) was achieved. Path analyses were performed with Statistica 6.0 software (StatSoft Inc. 2001). We transformed all variables (arcsine square root, for proportions; $\log x + 1$, for abundances) prior to analyses.

Due to configuration of the sampling framework, effects of environmental correlates and bird abundance on seed dispersal may have been estimated incorrectly due to presence of spatial autocorrelation in the studied variables (Keitt et al. 2002). Thus, to check for consequences of spatial constraints in the previous SEM, we fitted simultaneous autoregressive models (SAR; Keitt et al. 2002; see Supporting Information). We considered that the partial regression coefficients provided by SAR models represented the direct effects of habitat features, fruit abundance, and bird abundance on seed dispersal, free of autocorrelation constraints.

Results

Habitat Structure, Bird Abundance, and Seed Dispersal

The study systems differed strongly in habitat features, abundance of fruits available to frugivores, abundance of birds, and magnitude of seed dispersal (Table 2). The major fruiting species were *Ilex aquifolium* (Cantabrian forest, 58% of total crop), *Berberis hispanica* (Mediterranean shrubland, 83% of crop), and *Aristotelia chilensis* (Patagonian forest, 80% of crop). The frequency of occurrence of frugivorous birds was high in all transects (Table 2). The most frequent bird species were, in the Cantabrian forest, *Turdus iliacus* and *T. merula* (71% and 14% respectively, 1904 recordings), in the Mediterranean shrubland, *T. torquatus*, *Erithacus rubecula,* and *T. merula* (respectively, 56%, 18% and 12%, 1150 recordings), and in the Patagonian forest, *E. albiceps* (97%, 616 recordings).

Seed dispersal was widespread in the Cantabrian forest, but was undetected in some plots in the remaining systems (Table 2). The proportion of samples with seeds in the Cantabrian forest and Mediterranean shrubland and the number of seeds per trap in the Patagonian forest were greater in plots with more woody cover and higher fruit densities (Fig. 2). Nonetheless, the magnitude of seed dispersal was heterogeneous in low cover and fruit-poor patches, indicating that some seeds were deposited in even the most degraded patches in all studied landscapes (Fig. 2). Indeed, 13% of sampling quadrats where we found dispersed seeds occurred in plots with <20% forest cover in the Cantabrian forest, and 14.6% of dispersed seeds collected in the Patagonian forest occurred in plots with <30% forest cover.

Table 2. Average (SE) per-plot values of the abundance of frugivorous birds, abundance of fleshy fruits available to frugivores, occurrence (or abundance) of dispersed seeds, and percent forest and shrub cover in the Cantabrian forest, Mediterranean shrubland, and Patagonian forest.*

	Cantabrian forest	*Mediterranean shrubland*	*Patagonian forest*
Forest cover (%)	32.4 (2.7), 89	1.8 (0.6), 17	71.7 (3.3), 96
Shrub cover (%)	-	50.8 (1.6), 100	73.0 (2.8), 100
Fruits/m^2	138.2 (15.3), 85	73.7 (9.5), 97	24.1 (4.7), 65
Frugivorous birds	17.9 (2.2), 83	8.9 (1.5), 72	7.9 (0.5), 100
Prop. samples with seeds	0.54 (0.03), 100	0.12 (0.01), 74	-
Seeds/trap	-	-	1.8 (0.3), 69

**Value following SE is proportion of sampled plots with values > 0.*

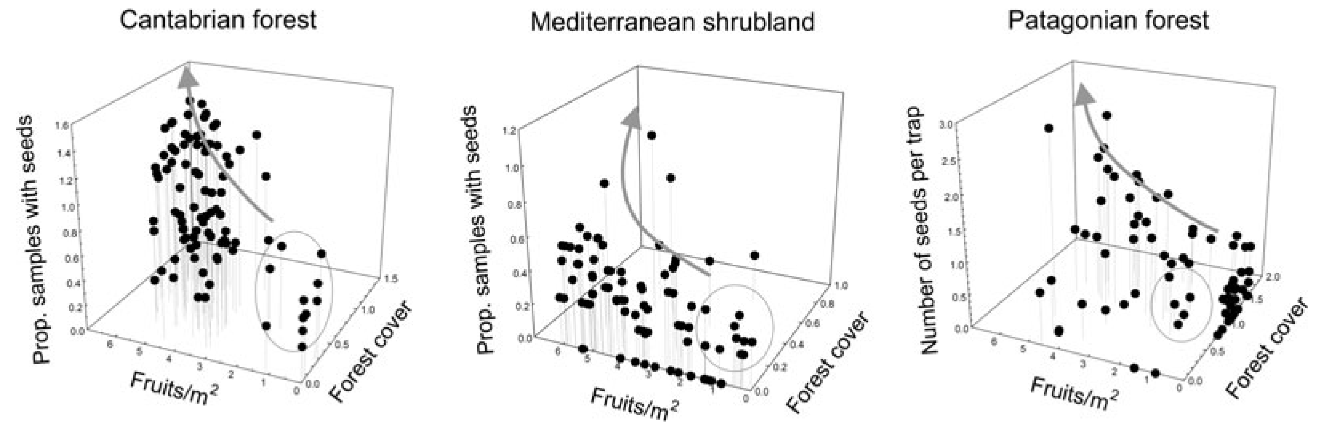

Figure 2. Magnitude of seed dispersal as a function of forest cover (arcsine transformed) and fruit abundance (log transformed) in the three studied ecosystems (dots, different plots along the sampling transects; arrows, general trends of increase in seed dispersal with forest cover and fruit abundance; ellipses, plots receiving different levels of seed deposition even with low forest cover or fruit availability [i.e., degraded patches]).

Determinants of Seed Dispersal

The SEM path coefficients showed a significant positive direct effect of bird abundance on seed dispersal in all systems (Fig. 3). Patches hosting higher bird densities received more dispersed seeds, although the effect of bird abundance on seed dispersal was weaker in the Patagonian forest than in the other systems. Forest and shrub cover and fruit abundance also showed significant direct effects on seed dispersal. As judged by the standardized regression coefficients (Fig. 3), these effects were stronger than those of bird abundance, although their sign and strength differed between systems. In the Cantabrian forest the effect of forest cover was strong and positive, indicating that more seed deposition occurred in plots with high cover, and irrespective of the abundance of fruits and birds. In the Mediterranean shrubland, seed dispersal was positively and significantly affected by the abundance of fleshy fruits, but negatively and marginally affected by shrub cover. This indicated that more dispersed seeds accumulated in fruit-rich patches, even when visited by low numbers of birds. It also suggested that, when controlling for effects of the remaining predictors, low shrub coverage favored seed deposition (SEM showed a positive, but nonsignificant, total effect of shrub cover on seed dispersal; see Supporting Information). A direct and even stronger positive effect of fruit abundance on seed dispersal was also found in the Patagonian forest, as were positive effects of forest and shrub cover that suggested some effect of denser vegetation patches on the individual activity of frugivorous birds.

In all systems the indirect effects of habitat features, fruit abundance, and bird abundance on seed dispersal accounted for a large portion of variability in seed deposition (Fig. 3; Supporting Information). In the Cantabrian forest, the abundance of birds depended on fruit abundance and forest cover, two intercorrelated variables. In the Mediterranean shrubland, the links of fruit abundance

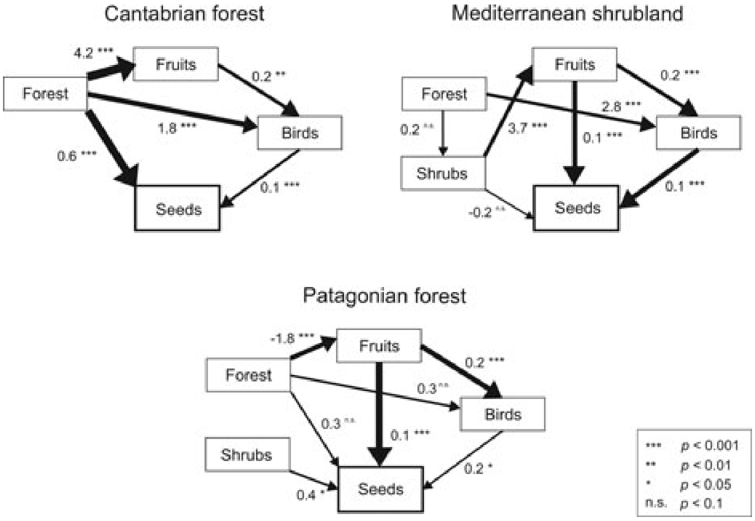

Figure 3. Structural equation models relating the frequency of occurrence or abundance of dispersed seeds (seeds) to the abundance of frugivorous birds (birds), abundance of fruits (fruits), tree-canopy cover (forest), and cover of understory shrubs (shrubs). The schemes represent the causal links included in the best-fit models and indicate the sign, magnitude, and degree of significance of the unstandardized, partial-regression coefficients (width of arrows is proportional to the value of each standardized coefficient; values of Akaike information criterion for the models of Cantabrian forest, Mediterranean shrubland, and Patagonian forest were 26.0, 35.8, and 35.3, respectively).

and forest cover to bird abundance indicated that more birds were seen in fruit-rich patches, mostly in areas of high shrub cover, but also in the scant patches with high forest cover even when they were devoid of fruits. In the Patagonian forest, birds were also more abundant in fruit-rich patches and, to some degree, under denser canopy cover, despite the fact that fruit production in the understory responded positively to openness of the canopy.

The SAR models relating seed dispersal to habitat features, fruit abundance, and bird abundance corroborated the effects suggested by previous SEM, free of spatial autocorrelation constrains. They showed the existence, in all study systems, of positive and significant effects of bird abundance on seed dispersal, as well as the relative effect of forest and shrub cover and fruit abundance (Supporting Information).

Discussion

The ecological importance of seed dispersal by birds in pristine and degraded habitats has been recognized for decades (e.g., Herrera 1985; reviewed in Sekercioglu [2006] and Whelan et al. [2008)]. Results of recent studies suggest a pivotal role for avian seed dispersers in providing a supporting ecosystem service in other temperate systems (Tellería et al. 2005; Lundberg et al. 2008). Our findings go beyond these previous works by showing the actual role of birds as seed dispersers within the context of environmental gradients found in real-world landscapes. Our results also show the relative influence of key environmental factors, such as habitat and resource availability, on the provision of the seed-dispersal function. Although the relative simplicity of the plant-frugivore systems we studied (relatively low richness of plant species and small coteries of bird dispersers) is a handicap in attempts to apply our results in more diverse systems, we argue that our results on how human-induced heterogeneity affects seed dispersal could be extrapolated to systems with impoverished frugivorous guilds dominated by generalist species (e.g., Muscarella & Fleming 2007; Pejchar et al. 2008).

Our data show the existence of a general (i.e., context-independent), positive relationship between magnitude of seed dispersal and abundance of frugivorous birds across all the landscapes we studied. Seed dispersal was linked to abundance of seed dispersers even after controlling for confounding effects of environmental variables that affect bird foraging and movement. In other words, many patches across the landscape, even some impoverished due to anthropogenic degradation and devoid of woody cover and fruits (Fig. 2), received dispersed seeds because of intense bird visitation. As suggested by the results of previous studies in the same or similar systems, these degraded patches probably have some characteristics that override the reluctance of birds to visit the degraded matrix, such as their proximity to well-conserved patches (Armesto et al. 2001; Clough et al. 2009) or the presence of perching elements, such as rocky outcrops or isolated remnant trees (García 2001; Herrera & García 2009).

Structural-equation models suggested that canopy-dense patches in the Cantabrian forest and fruit-rich patches in the Mediterranean shrubland and Patagonian forest accumulated, disproportionately, frugivore activity and hence seed deposition, even when they were visited by few birds. These direct effects on frugivore activity were even stronger than that of bird abundance per se in determining the spatial pattern of seed dispersal. As suggested for other frugivores, protective forest patches that serve as roosting sites and fruit-rich neighborhoods that provide resources with a low cost of mobility, promote longer permanency times among frugivores, and lead to large clumps of dispersed seeds beneath or around them (Russo & Augspurger 2004; García et al. 2009). In any case, and at least in the Iberian systems, the role of woody cover or fruit abundance as major determinants of seed dispersal could partially weaken because of late postdispersal seed losses. For example, seed predation is stronger in woody-covered, fruit-rich microhabitats than in open patches (García et al. 2005*b*; Matías et al. 2009).

Besides the above-mentioned direct effects, our data show strong indirect effects of habitat features, fruit abundance, and bird abundance on seed dispersal. For example, some patches received more seeds because they were visited throughout the season by more birds that track forest cover and fruit availability at the landscape scale (see also Rey 1995; Tellería et al. 2005). Finally, the three-step causal cascades we found suggest that a significant part of seed fall derived from the concurrence of many birds tracking fruit resources with spatial distributions that depended largely on the amount of forest or shrub cover.

Conservation and Management of Bird-Supplied Seed Dispersal

A prerequisite for discussing the role of frugivorous birds in terms of ecosystem service and its conservation is to address the actual importance of seed dispersal in the whole process of within- and between-patch vegetation dynamics (Bengtsson et al. 2003). In this sense, previous research demonstrates that seed dispersal is a major driver of the regeneration process in many studied plants (García et al. 2005*b*; Mendoza et al. 2009). Thus, we assume the links among the environment, birds, and seeds demonstrated here will have a concomitant effect on the recruitment patterns of fleshy-fruited species, and hence, on the many economically and noneconomically valuable services dependent on woody regeneration across landscape mosaics. Further analyses (e.g., Hougner et al. 2006) are required to value bird-generated seed dispersal in explicit economic terms.

On the basis of our findings, we propose three starting points for conservation strategies targeting seed dispersal as a pivotal process in ecosystem preservation or restoration. First, consider the abundance of frugivorous birds a landscape-scale surrogate of seed dispersal because this parameter predicts at least part of the spatial variability of seed deposition. The fact that bird abundance was the only consistent predictor of seed rain across the three study systems suggests this consideration could be generalizable (see also Pejchar et al. 2008). Despite bird abundance being a poorer predictor of seed rain than woody cover and fruit availability, the actual occurrence of a generalized link between birds and dispersed seeds encourages the use of bird abundance as a coarse-grain indicator of the patches within a given landscape with the highest conservation value for ecosystem service (i.e., those patches more visited by birds; see Sanford et al. [2008] for a similar approach with services provided by ants.) Knowing whether bird abundance may be used as an indicator of seed dispersal at larger temporal (e.g., different years in a given habitat) and spatial (e.g., different habitats or localities in a given region) scales would require further study, but the role of environmental correlates in frugivory must always be considered. In fact, local fruit availability, and not bird abundance, could be the best predictor of seed dispersal at a regional scale, given the large-scale tracking ability of frugivorous birds in systems such as the Cantabrian forest and the Mediterranean shrubland (García & Ortiz-Pulido 2004).

Second, target woody cover and fruit resource availability as the key landscape features that ultimately drive seed-fall patterns. Keeping in mind the relative role of these environmental correlates in predicting the occurrence of dispersed seeds, any landscape-scale management of seed dispersal must consider both the composition and spatial configuration of original habitat patches within the degraded matrix. In landscape-composition terms, maintaining or promoting within-habitat, dispersal-friendly features in regard to woody cover and fruit abundance are crucial measures for attracting large quantities of birds into remnant habitat patches (Tellería et al. 2005). In landscape-configuration terms, a variegated structure in which different-sized remnant patches of original habitat (i.e., patches containing developed forest cover and fleshy fruits) are intermingled with the degraded matrix, may maintain high levels of connectivity for seed dispersal due to the great vagility and large-scale resource-tracking ability of frugivores (Bodin et al. 2007).

Third, consider avian frugivores mobile links for seed dispersal in all ecosystems because they connect patches with different degrees of degradation and of different habitat quality via the deposition of seeds. Birds guarantee seed input into some degraded patches, a fact that represents the trigger for recovery of woody vegetation. Thus, preservation of the seed-dispersal process and its mobile agents should be considered a tool for passive and hence low-cost ecological restoration (Howe & Miriti 2004). In addition, in landscape planning, structural traits of degraded patches—such as isolated remnant trees or shrubs—or their degree of adjacency to the original, well-preserved patches must be considered as key elements of internal ecological memory that maintain ecosystem resilience (Bengtsson et al. 2003).

We believe temperate frugivorous birds should be classified as effective suppliers of the seed-dispersal ecosystem service at the landscape scale. We encourage conservationists and land managers to explicitly consider such a classification if they aim to develop integrative plans focused on specific species or target habitats and on the ecological interactions driving ecosystem fluxes.

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Supporting Information

Additional details and results of spatial autoregressive models (Appendix S1) and path analysis (Appendix S2) are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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