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REVIEW

Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration

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ABSTRACT

Seed dispersal mutualisms with scatter-hoarders play a crucial role in population dynamics of temperate large-seeded trees. These behaviors shape seed dispersal patterns, which can be applied to conservation of populations, communities, and even ecosystems dominated by large-seeded trees. We draw on a growing body of literature to describe the ecological context and consequences of scatter-hoarding as a seed dispersal mechanism. We synthesize the quantitative literature on the interaction between members of the avian family Corvidae (crows, ravens, jays, magpies, and nutcrackers) and nut-bearing trees such as pines (*Pinus* spp.) and oaks (*Quercus* spp.) to examine unique aspects of avian scatter-hoarders as seed dispersers. During the scatter-hoarding process, seed selectivity, transportation distance, hoarding frequency, and cache placement affect seed dispersal effectiveness, a measure of the quantity and quality of dispersal. Case studies from around the world highlight the role of corvid seed dispersal in population dynamics of trees, and how the birds' scatter-hoarding behavior can be facilitated for the restoration of oak- and pine-dominated habitats. This mutualism, which provides many plant species with long-distance, high-quality seed dispersal, will likely become even more important for conservation of oak and pine ecosystems as suitable climates shift rapidly in the decades ahead. This ecosystem service provided by corvids could therefore serve as an efficient conservation tool.

Keywords: Corvidae, ecosystem engineer, habitat restoration, *Pinus*, *Quercus*, scatter-hoarding, seed dispersal

Almacenamiento disperso en córvidos dispersores de semillas de robles y pinos: revisión de un mutualismo ampliamente distribuido y su utilidad para la restauración de hábitat

RESUMEN

Los mutualismos relacionados con la diseminación de semillas por parte de animales que almacenan alimentos en lugares dispersos, juegan un rol crucial en la dinámica poblacional de los árboles que producen semillas de gran tamaño en zonas templadas. Dichos comportamientos de almacenamiento moldean los patrones de dispersión de semillas, los cuales pueden ser fundamentalmente implementados en la conservación de poblaciones, comunidades e inclusive en ecosistemas dominados por árboles de semillas de gran tamaño. En la presente revisión, contribuimos al creciente conjunto de literatura científica que describe el contexto ecológico y las consecuencias del almacenamiento disperso como un mecanismo de diseminación de semillas. Además, sintetizamos la literatura cuantitativa sobre la interacción entre miembros de la familia de aves *Corvidae* (cuervos, arrendajos, urracas y cascanueces) y árboles que producen conos como los pinos (*Pinus* spp.) y bellotas como los robles (*Quercus* spp.), para examinar aspectos únicos de la diseminación de semillas mediante el almacenamiento disperso por parte de las aves anteriormente reseñadas. Durante el proceso de almacenamiento, la selectividad de las semillas, la distancia de transporte y la frecuencia y ubicación del almacenamiento logran afectar la efectividad de la dispersión, parámetro que constituye una medida de la cantidad y calidad de la misma. Diversos estudios de caso en todo el mundo, resaltan el importante papel de la dispersión de semillas por parte de córvidos en la dinámica poblacional de los árboles y logran describir la forma en la cual el comportamiento del almacenamiento disperso de las aves, puede ser beneficioso para restaurar hábitats dominados por pinos y robles. Asimismo, este mutualismo que otorga a muchas especies de plantas que suelen tener dispersión de sus semillas a larga distancia, una alta calidad en los aspectos relacionados con diseminación de semillas, probablemente tenga aún más importancia en la conservación de ecosistemas de pinos y robles con el aceleramiento del cambio climático en las próximas décadas. Este servicio ecosistémico brindado por los córvidos podría servir como una herramienta eficiente de conservación.

Palabras clave: Almacenamiento disperso, Corvidae, dispersión de semillas, ingeniería del ecosistema, *Pinus*, *Quercus*, restauración de hábitat

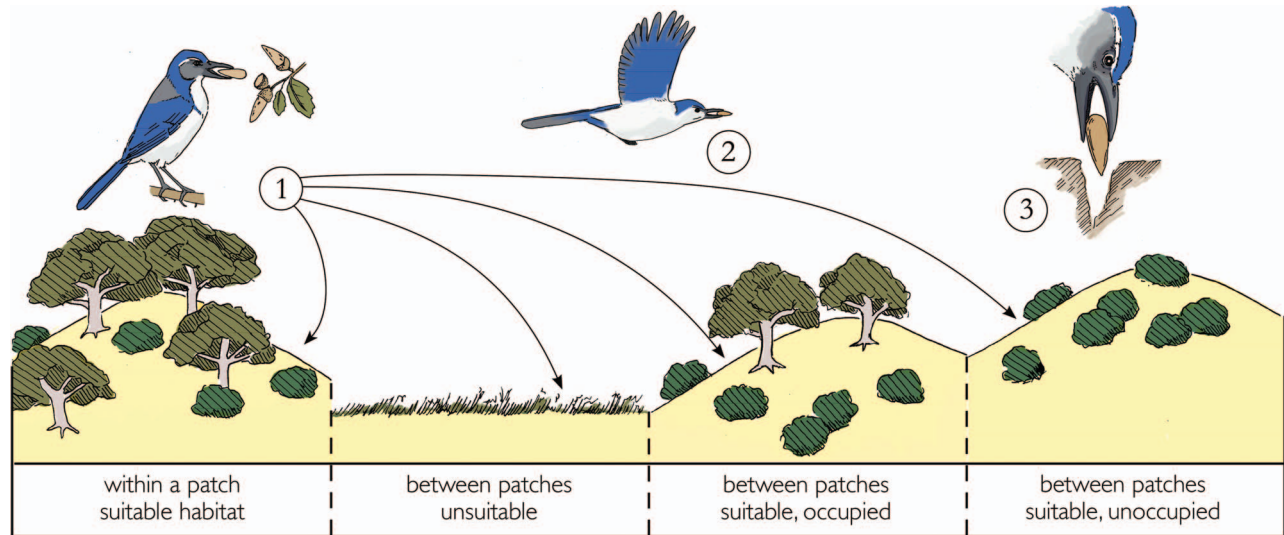


FIGURE 1. Key steps of the scatter-hoarding process: (1) seed selection, (2) transportation, and (3) deposition. Seeds can be cached within and between patches of suitable habitat already colonized by the species, in a patch of unsuitable habitat, or in suitable habitat that can be colonized. Illustration credit: Emily Underwood

It is not extravagance, but good investment, for the oaks to provide subsistence for a continuing population of animal associates. (Grinnell 1936)

INTRODUCTION

Seed dispersal fundamentally influences population and community dynamics, and plants often rely on animals as dispersal vectors (Howe and Smallwood 1982). Similarly, many animals that serve as dispersal vectors rely on plant seeds both for subsistence and to store for subsequent consumption. In fact, stored food can provide a substantial portion of the hoarders' diet, sometimes >90%, especially during winters when food availability is limited and bird mortality is high (Lanner 1982, Vander Wall 1990, Balda and Kamil 1998, Derbyshire et al. 2015). This interdependence with large-seeded plants is particularly true for birds in the nearly cosmopolitan family Corvidae, which includes >120 species, including jays, crows, and magpies (Goodwin 1983, Vander Wall 1990). Many corvid species store seeds in the ground by placing them in spatially distributed caches, a behavior termed "scatter-hoarding." This form of seed dispersal mutualism has important, cascading ecological and evolutionary consequences for both plants and birds and thus serves as an excellent model system for the role of animal behavior in seed dispersal.

Here, we provide a broad introduction to seed dispersal by animals. We describe the paradigms of seed dispersal effectiveness (Schupp 1993, Schupp et al. 2010) and long-distance dispersal (Nathan and Muller-Landau 2000, Nathan 2006, Nathan et al. 2008) and use them to frame

our synthesis of the large body of literature on scatter-hoarding by corvids. First, following the behavioral sequence from seed acquisition to deposition in the ground (Figure 1), we describe how seed dispersal effectiveness and distance are affected by the birds' behavior. We then discuss the ecosystem-wide consequences, as well as behavioral and morphological adaptation by plants, and use case studies from around the globe to illustrate the broad geographic distribution of this important form of animal-facilitated seed dispersal (Figure 2). Finally, we illustrate the application of the birds' ecosystem services in the context of habitat restoration, with examples from oak restoration in Mediterranean Spain and in California, USA, and from pine restoration in western North America.

SEED DISPERSAL AND ANIMAL BEHAVIOR

Seed dispersal by animals is common and takes a variety of forms: 40–90% of woody species in tropical rainforests and 25–80% of temperate plant species rely on seed dispersal facilitated by animals, or zoochory (Howe and Smallwood 1982, Jordano 2000). Zoochory is often divided into categories based on the way in which seeds are transported by the disperser. For example, endozoochory is dispersal by ingestion and subsequent regurgitation or defecation (Jordano 2000). Other seeds have structures that allow them to adhere to the exterior of their disperser (epizoochory), which tend to be furry or woolly animals (Will and Tackenberg 2008). Finally, some animals perform synzoochory, actively picking up seeds and depositing them elsewhere (Hulme 2002, Vander Wall and Beck

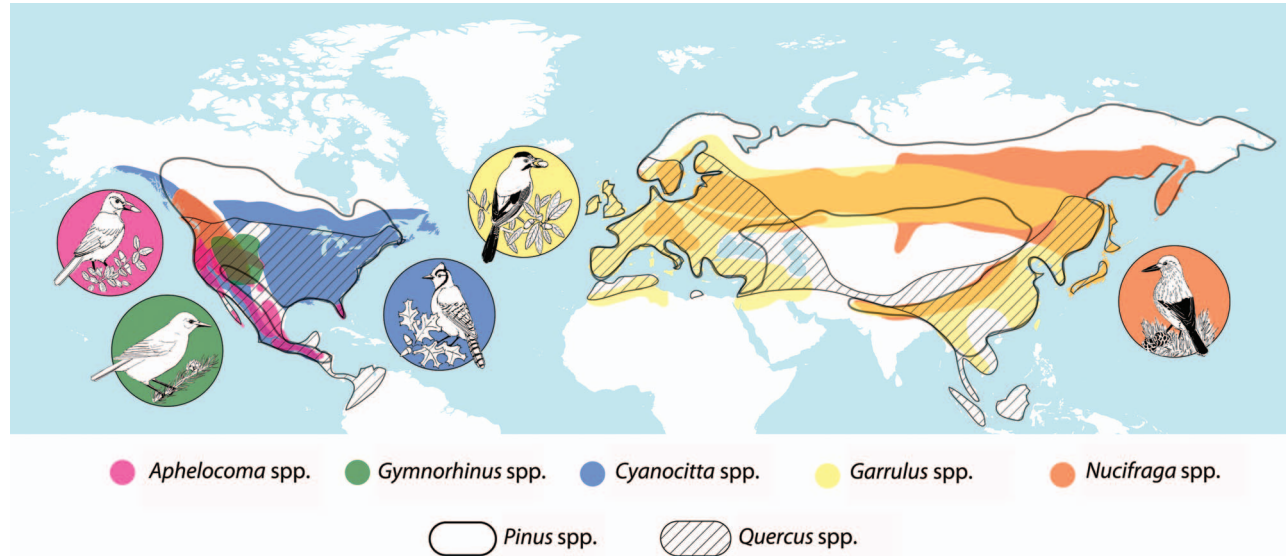


FIGURE 2. Spatial extent of the seed dispersal mutualism between oak and pine trees and corvids. Outlines indicate the approximate global distributions of *Quercus* (adapted from Logan 2005) and *Pinus* (adapted from Critchfield and Little 1966, Fang et al. 2011). Colors indicate species ranges of corvids in genera that dominantly scatter-hoard seeds (data from BirdLife International, 2012). Illustration credit: Emily Underwood

2012). In each of these forms of zoochory, the processes of seed acquisition, transport, and deposition differ, thus affecting the resulting spatial distribution of dispersed seeds.

The spatial patterns of seed deposition are primarily shaped by the behavior and movement of their dispersers. To estimate dispersal rates and distances for endozoochorous and epizoochorous dispersal, for example, seed-specific gut passage or attachment and detachment rates are combined with movement patterns of the animals (Westcott and Graham 2000, Will and Tackenberg 2008, Côrtes and Uriarte 2013). Because animals rarely use the landscape in a random manner—for example, a disperser may avoid open spaces—differences in habitat composition and usage patterns can lead to differential seed deposition over a range of spatial scales (Alcántara et al. 2000, Rodríguez-Pérez et al. 2012). Locations used frequently, such as sleeping sites and roosts, can experience higher seed deposition rates, leading to spatial clumping of seedlings (Wenny and Levey 1998, Russo et al. 2006). Thus, to identify the aspects of animal behavior that are relevant in shaping seed dispersal patterns, researchers often compare the movement and foraging behavior of dispersers with spatial seed deposition patterns (Wenny 2001, Russo et al. 2006, Côrtes and Uriarte 2013). Despite recent advances in modeling of behavioral mechanisms involved in seed dispersal by endozoochory and epizoochory, our general understanding of the role of behavior in zoochory, and particularly of scatter-hoarding, still lags behind that of abiotic dispersal by wind or water (Cousens et al. 2010).

QUANTIFYING ZOOCHORY: DISPERSAL EFFECTIVENESS AND DISTANCE

In seed-disperser communities, disperser species vary in their seed dispersal effectiveness, defined as their contribution to the plant's fitness (Schupp 1993, Schupp et al. 2010). Seed dispersal effectiveness is a quantitative measure comprising 4 components: (1) visitation rate and (2) number of seeds acquired per visit, which together determine dispersal quantity; along with (3) treatment in the mouth and gut and (4) aspects of seed deposition that affect the probability of seed and seedling survival, as well as emergence and subsequent growth, which together determine dispersal quality. Characterizing seed dispersal effectiveness allows for comparisons of the contributions of different members of the disperser community to plant demography and fitness. For example, Figuerola et al. (2003) compared the seed dispersal effectiveness of several waterfowl species when dispersing aquatic widgeongrass (*Ruppia maritima*) and found that gut passage in all bird species enhanced seed germination rate, enhancing dispersal quality. They also found a positive correlation between dispersal quantity and quality of each disperser, specifically between the average number of seeds in droppings and the proportion of seeds that germinated from those samples. By quantifying seed dispersal effectiveness and understanding the processes that affect its components, ecologists can learn about the contribution of dispersal vectors to the fitness of a plant species (Schupp et al. 2010).

Dispersal distance, which quantifies movement away from the source plant, is not explicitly included in the

quality and quantity metrics of the seed-dispersal-effectiveness framework described above. Schupp et al. (2010) argued that the contribution of dispersal distance to plant fitness in terms of seed dispersal effectiveness is unclear. They pointed out the lack of an empirical framework within which the fitness benefits from long-distance dispersal might be compared with those from local dispersal. Distance is clearly important for colonization, but the likelihood of long-distance dispersal events is difficult to quantify (Nathan and Muller-Landau 2000). Nonetheless, the outcomes associated with dispersal over long distances are of disproportional importance to large-scale population dynamics, because they allow for the colonization of new areas and, thus, the expansion and movement of species ranges (Cain et al. 2000). We agree with Schupp et al. (2010) that the inclusion of distance will provide the most groundbreaking addition to their seed-dispersal-effectiveness framework, given that the direct fitness benefits of long-distance dispersal are illustrated in several well-studied systems (Lesser and Jackson 2013, Caughlin et al. 2014).

In heterogeneous landscapes, the fitness benefits of dispersal distance are different for within-patch dispersal than for dispersal among habitat patches. Within patches, increasing dispersal distances can reduce density-dependent mortality that can be caused by intraspecific competition by specialized pathogens or predators (Janzen 1970, Connell 1971, Augspurger and Kelly 1984). The movement of seeds among patches or populations, or long-distance dispersal, plays an important role in metapopulation dynamics in that it facilitates gene flow, the establishment of novel populations, spatial synchrony and the potential for population rescue, and range shifts in response to environmental variation (Liebhold et al. 2004, Bohrer et al. 2005, Nathan 2006, Engler and Guisan 2009). For example, Lesser and Jackson (2013) used parentage analysis of trees in newly established stands of ponderosa pine (*Pinus ponderosa*) to show that repeated long-distance dispersal events over the first century of colonization were necessary for population establishment and initial population growth, and as evidence for gene-flow benefits of long-distance dispersal in comparison to wind pollination.

Long-distance dispersal may also lead to high seed dispersal effectiveness by increased dispersal quality. Large dispersal distances can facilitate directed dispersal, the arrival of a disproportionate number of seeds in locations that are more suitable for seed germination and seedling growth than in surrounding habitat (Howe and Smallwood 1982, Wenny and Levey 1998, Wenny 2001). For example, Spiegel and Nathan (2007) studied how White-spectacled Bulbuls (*Pycnonotus xanthopygos*) and Tristram's Starlings (*Onychognathus tristramii*) disperse seeds of the desert shrub *Ochradenus baccatus* in Israel. The data show that

the dispersal services provided by each species differed owing to differences in the frequency with which each foraged from the different plant species and in species-specific gut retention times, with consequences for subsequent seed germination and dispersal distances: One species mainly dispersed seeds within habitat patches, whereas the other moved seeds to distant patches. The authors thus argued that dispersal distance should be explicitly integrated into studies of seed dispersal effectiveness, because plants reap additional, direct fitness benefits from dispersers that carry seeds among habitat patches. Several studies have shown that habitat preferences by dispersers can result in increased long-distance dispersal (Gómez 2003, Lenz et al. 2011). To reach preferred habitat for foraging or seed caching, many birds traverse nonfavored areas before depositing seeds. In such heterogeneous habitats, plant benefits from long dispersal distances may well be associated with directed dispersal (Bossema 1979, Wenny 2001).

SCATTER-HOARDING CORVIDS AS SEED DISPERSERS

Scatter-hoarding animals actively select seeds at the source plant, transport them in the mouth or bill, and deposit them in small, spatially distributed caches (Figure 1). Larder-hoarders, by contrast, place all food items in a few central locations. Most corvids scatter-hoard food to recover it later for consumption (Goodwin 1983, Balda and Kamil 1989, 2006, Madge and Burn 1994, de Kort and Clayton 2006, Tomback 2016), a phenomenon that has been studied in communities of large-seeded trees throughout the Northern Hemisphere (Table 1 and Figure 2). Crows and ravens (*Corvus* spp.) and jays in the genus *Perisoreus* preferentially store carrion and animal prey over seeds (James and Verbeek 1983, Waite and Reeve 1992, Bugnyar and Kotrschal 2002), whereas most jays (*Aphelocoma*, *Calocitta*, *Cyanocitta*, *Garrulus*, and *Gymnorhinus* spp.) and nutcrackers (*Nucifraga* spp.) predominantly store seeds (Goodwin 1983, Madge and Burn 1994, Tomback 2016).

Scatter-hoarding turns into seed dispersal when seeds are not recovered by the hoarder. Despite formidable spatial memory, corvids fail to recover some of their caches (Balda and Kamil 1992, Balda et al. 1997) or simply cache more nuts than they will need in the following winter and spring (Tomback 1982, DeGange et al. 1989). The hoarder also may be forced out of its territory or perish, leaving an even higher number of seeds in caches, or retrieve the cotyledons after the seedling is established (Bossema 1979, Vander Wall 1990). Whatever the reason for the cache being abandoned, if the deposition location is suitable for germination and subsequent establishment, the source plant ends up benefiting (Tomback 1982, 2016, Vander Wall 1990, Whelan et al. 2008).

In the northern temperate zone, many broadleaved tree and shrub species rely exclusively on scatter-hoarders for seed dispersal, including walnuts (*Juglans* spp.), hickories (*Carya* spp.), hazelnuts (*Corylus* spp.), beeches (*Fagus* spp.), chestnuts (*Aesculus* spp. and *Castanea* spp.), and oaks (*Quercus* spp.) (Vander Wall 1990). Furthermore, of the estimated 100 species in the genus *Pinus*, 19 have evolved large, wingless seeds adapted to dispersal by hoarders (Tomback and Linhart 1990). In addition, at least 3 species with winged seeds (*P. jeffreyi*, *P. lambertiana*, and *P. coulteri*) are dispersed secondarily by rodent and corvid hoarders after initial wind dispersal (Vander Wall and Longland 2004, Tomback 2016). The prominent role of this dispersal mutualism is also illustrated by the broad geographic distribution of the interaction (Figure 2), as well as by the adaptations of both dispersers and plants.

Because scatter-hoarders are both seed predators and dispersers, plants have developed adaptations in seed morphology, chemical defenses, and annual seed-production patterns that maximize the mutualistic benefit from their animal partners (Vander Wall 2010, Vander Wall and Beck 2012). They generally have large seeds that contain high levels of carbohydrates and moderate levels of lipids and proteins, thus quickly satiating animals. Rapid satiation of the hoarders, in turn, increases the probability that seeds are stored and not just consumed (Tomback 1982, Tomback and Linhart 1990, Koenig and Benedict 2002, Vander Wall 2010, Vander Wall and Beck 2012).

Similarly, long handling times necessary to process seeds are thought to encourage scatter-hoarding over immediate consumption. Thick seed coats require substantial effort to remove. The more time it spends eating at the source, the longer the animal is exposed to predators and the more seeds other competitors can transport away (Andersson and Krebs 1978, Vander Wall 2010). Once in the ground, seeds are almost odorless and often hard to find by other seed predators, thus reducing secondary losses (Borchert et al. 1989). Many seeds contain protective chemicals; acorns, for example, contain tannins—phenolic compounds that are difficult to digest but that allow the seeds to be stored for an extended time without rotting. In general, however, acorns are recalcitrant and do not remain viable in the seed bank for more than a year (Fleck and Tomback 1996, Fleck and Woolfenden 1997). This suite of morphological adaptations quite likely evolved in response to seed dispersal by scatter-hoarders (Vander Wall 2010).

The behavioral sequence of scatter-hoarding highlights 3 points at which corvids affect the fitness of dispersed plants (Figure 1). When selecting seeds at the tree, transporting them to caching locations, and depositing the seeds in the cache, the birds' behavior can change the likelihood of seed survival and subsequent establishment. Below, we describe each step in detail and then discuss

how mast-seeding may affect scatter-hoarding and how the consequences of corvid seed dispersal can affect whole ecosystems.

Seed Selectivity: Crop Size, Predispersal Predation, and Seed Characteristics

Variation in seed characteristics within and among tree species can affect seed dispersal because corvids are selective when choosing seeds for hoarding. When seed crops are large and seeds are not limiting, birds selectively forage on, and therefore disperse, trees with seed characteristics that they prefer. For example, arthropods and fungi often damage pine cones and acorns during maturation (Espelta et al. 2009). Within trees, many birds inspect seeds and avoid ones with obvious damage caused by insects whose larvae eat the cotyledons, which are often the most nutritious part of the seed (Bossema 1979, Darley-Hill and Johnson 1981, Fleck and Woolfenden 1997, Hubbard and McPherson 1997). Despite low availability (11%) of viable seeds on American beech (*Fagus grandifolia*) trees, Blue Jays (*Cyanocitta cristata*) transported and cached viable seeds only (Johnson and Adkisson 1985). After visual inspection, the birds assess seeds by handling them with their bill, lifting and rattling them in the process, which also allows them to exclude seeds that have been compromised by arthropods but show no exterior traces (Vander Wall and Balda 1977, Dixon et al. 1997, Hubbard and McPherson 1997, Langen and Gibson 1998, Langen 1999). Similarly, Clark's Nutcrackers (*Nucifraga columbiana*) discarded $\geq 4.5\%$ of pinyon pine seeds, many of which were subsequently determined to be spoiled (Vander Wall and Balda 1977). Birds not only ignore damaged seeds within a tree; sometimes they avoid trees and entire stands with low-quality cones or those affected by insects (Christensen and Whitham 1991, 1993, Christensen et al. 1991). The avoidance of damaged seeds by scatter-hoarding birds enhances the quality of seed dispersal, because the proportion of viable seeds that are dispersed is higher than the proportion present on the tree.

Size and chemical composition affect corvid preferences for acorns of different oak species. Darley-Hill and Johnson (1981) reported that Blue Jays in Virginia removed the seeds from pin oak (*Q. palustris*), black oak (*Q. velutina*), willow oak (*Q. phellos*), and American beeches while ignoring nearby white oaks (*Q. alba*) and northern red oaks (*Q. borealis*) that were also carrying large acorn crops; they speculated that the large diameter of red oak acorns and the early germination of white oak acorns may have deterred the birds. Scarlett and Smith (1991) found a similar pattern in Blue Jays in Arkansas, which avoided the large acorns of white, red, and English oaks (*Q. robur*) while foraging on smaller acorns of willow, pin, black, and post oaks (*Q. stellata*). In subsequent experiments, the

TABLE 1. Summary of studies that quantified symbiotic interactions between scatter-hoarding corvids and seed-bearing plant species. Errors given represent one standard deviation of the mean.

Scatter-hoarder	Location and habitat	Tree species	Dispersal parameters	Symbiotic benefit	Reference ^a
Genus <i>Aphelocoma</i>					
Western Scrub-Jay (<i>Aphelocoma californica</i>)	California, USA; oak woodland	<i>Quercus douglasii</i> , <i>Q. lobata</i> , <i>Q. agrifolia</i>	Caching effort: 5,000 acorns	Dominant seed disperser	1
Florida Scrub-Jay (<i>A. coerulescens</i>)	Florida, USA; xerophytic scrub dominated by oaks	<i>Q. inopina</i> , <i>Q. geminata</i> , <i>Q. chapmanii</i>	Caching frequency: 30–90 day ⁻¹ (5,000 yr ⁻¹) Cache recovery: 27% within year	Unclear, as oaks generally reproduce by cloning; potential long-distance dispersal	2
Island Scrub-Jay (<i>A. insularis</i>)	Santa Cruz Island, California, USA; oak chaparral and woodland	<i>Q. pacifica</i> , <i>Q. agrifolia</i>	Caching frequency: 7.2 hr ⁻¹ (4,500 yr ⁻¹) Mean distance: 38.5 m Maximum distance: 400 m Caching locations: below vegetation in chaparral and coastal sage brush	Dominant seed disperser; long-distance dispersal; directed dispersal	3
Mexican Jay (<i>A. wollweberi</i>)	Arizona, USA; oak woodland	<i>Q. emoryi</i>	Acorn selectivity: avoidance of parasitized acorns	Enhanced seed viability	4
Genus <i>Corvus</i>					
Rook (<i>Corvus frugilegus</i>)	Poland; agricultural areas and human settlements	<i>Juglans regia</i>	Maximum distance: >1,000 m Seedling density yr ⁻¹ : 19.6 ± 2.8 seedlings ha ⁻¹ Caching location: agricultural fields, recently abandoned fields, old fields	Long-distance dispersal; enhancement of seed germination and establishment; colonization of novel habitat	5
Hawaiian Crow (<i>C. hawaiiensis</i>)	Hawaii, USA (Big Island and Maui; in captivity)	14 native plants	Carried and cached seeds of each species; preferred caching large seeds	Extant dominant seed disperser; absence affects plant community composition	6
Genus <i>Cyanocitta</i>					
Blue Jay (<i>Cyanocitta cristata</i>)	Virginia, USA; mosaic of residential, agricultural, and mature forest habitats	<i>Q. palustris</i> , <i>Q. phellos</i> , <i>Q. velutina</i> , <i>Fagus grandifolia</i>	Maximum distance: 1,900 m Average distance: 1,100 m Proportion of acorn crop cached: 54% (133,000 acorns / ≥9 jays) Caching location: open soil, lawns	Long-distance dispersal; dominant seed disperser; acorn viability; enhanced germination and seedling survival	7
	Milwaukee, USA; agricultural area, wetlands, and mature forest	<i>F. grandifolia</i>	Seed selectivity Maximum distance: ~4,000 m	Enhanced seed viability; long-distance dispersal	8
	Iowa, USA; grassland, regenerating woodland in old field, and mature forest	<i>Q. velutina</i> , <i>Q. ellipsoidalis</i> , <i>Q. muehlenbergii</i> , <i>Q. alba</i>	Caching location: canopy gaps, woodland Increased caching in burned area	Enhanced seedling establishment; colonization of newly available habitat	9
	Maine, USA; mixed deciduous–coniferous forest	<i>Castanea dentata</i>	Only active disperser Maximum distance: ~300 m Spread of reintroduced species	Dominant seed disperser; long-distance dispersal; (re)colonization of newly available habitat	10

TABLE 1. Continued.

Scatter-hoarder	Location and habitat	Tree species	Dispersal parameters	Symbiotic benefit	Reference ^a
Steller's Jay (<i>C. stelleri</i>)	Nevada, USA; open yellow pine forest	<i>Pinus lambertiana</i>	Average distance: 203.7 ± 104.5 m Maximum distance: 370 m Average cache depth: 1.5 cm Caching location: closed-canopy pine forest, away from shrubs	Long-distance dispersal; enhanced germination; reduced postdispersal predation by rodents	11
	British Columbia, Canada; oak savanna	<i>Q. garryana</i>	Maximum distance: 600 m (anecdotally 1,000 m)	Long-distance dispersal	12
Genus <i>Garrulus</i>					
Eurasian Jay (<i>Garrulus glandarius</i>)	The Netherlands; agricultural area with forest islands	<i>Q. robur</i> , <i>Q. rubra</i> , <i>Corylus</i> spp., <i>Fagus</i> spp.	Acorn selectivity Maximum distance: 300 m (anecdotally several km) Caching location: edge of shrub Diet composition	Enhanced acorn viability; long-distance dispersal; enhanced germination and seedling survival; reduction of oak defoliators	13
	Southwestern Germany; calcareous grasslands (mowed vs. untouched)	<i>Q. petraea</i> , <i>Corylus avellana</i>	Caching and recaching activity Maximum distance: ~300 m Caching location: mowed grass	Reduced seed predation; long-distance dispersal; enhanced germination; facilitated establishment in disturbed area	14
	Eastern Germany; pine afforestation invaded by oaks	<i>Q. petraea</i>	Compared age distribution of oak and pine population Jays move only acorns, not pine seeds in this area	Competitive advantage in early stage of succession; rapid establishment in canopy gaps, clear-cut areas	15
	Southeastern Spain; mosaic of mixed temperate forest, open pine wood, and pine afforestation	<i>Q. ilex</i>	Maximum distance: 1,000 m Average distance: 262.9 ± 195.1 m Median distance: 200 m Caching location: open pine wood and pine afforestation	Long-distance dispersal; habitat selectivity; reduction of postdispersal predation	16
	Germany; temperate region, natural and agricultural areas	<i>Quercus</i> spp.	Review of old German silviculture literature Density of jay-planted oaks: 80–6,000 trees ha ⁻¹	Long-distance dispersal; establishment and rejuvenation of oak stands in abandoned fields; 60–90% of high wood-production quality	17
	Southeastern Spain; Mediterranean mosaic of shrubs, pines, active and old agricultural fields	<i>Q. ilex</i> , <i>Q. suber</i>	Maximum distance: 545.4 m Average distance: 68.6 ± 73.57 m Caching location: recently abandoned fields, roads, pines	Long-distance dispersal; habitat selectivity	18

TABLE 1. Continued.

Scatter-hoarder	Location and habitat	Tree species	Dispersal parameters	Symbiotic benefit	Reference ^a
	Central Spain; oak forests and <i>dehesas</i> (managed oak savanna)	<i>Q. ilex</i>	Caching location (forest): shrubs, herb tufts Caching location (<i>dehesa</i>): canopy, herb tuft, open areas Maximum caching distance: >700 m Preference for large acorns (forest)	Habitat selectivity; long-distance dispersal; seed selectivity	19
Genus <i>Gymnorhinus</i>					
Pinyon Jay (<i>Gymnorhinus cyanocephalus</i>)	Arizona, USA; pinyon–juniper woodland	<i>P. edulis</i> , <i>P. ponderosa</i>	Maximum distance: ~1,000 m Caching location: south side of trees (warmer areas)	Long-distance dispersal; enhanced seed germination or seedling establishment	20
	New Mexico, USA; pinyon–juniper woodland	<i>P. edulis</i>	Maximum seed load: 56 trip ⁻¹ Seed caching effort: ≥120 day ⁻¹	Dominant seed disperser	21
	Arizona, USA; pinyon–juniper woodland	<i>P. edulis</i>	Seed selectivity Maximum dispersal distance: 7,000 m	Enhanced seed viability; long-distance disperser	22
	Arizona, USA; pinyon–juniper woodland	<i>P. edulis</i> , bird mix in feeders	Cache location: 14% of caches in ground	Not evident	23
Genus <i>Nucifraga</i>					
Eurasian Nutcracker (<i>Nucifraga caryocatactes</i>)	Engadine, Switzerland; subalpine conifer forest	<i>P. cembra</i>	Pine invasion of abandoned pastures and newly available habitat above the treeline	Dominant seed disperser; colonization of novel habitat	24
	Engadine, Switzerland; subalpine conifer forest	<i>P. cembra</i>	19–30% of trees occur in multitrunk clusters, a consequence of nutcracker caches	Important seed disperser; potential colonization of novel habitat	25
	Heilongjiang Province, China; pine–hardwood forest	<i>P. koraiensis</i>	Maximum distance: 4,000 m Cache depth: 2.5–3.5 cm Cache location: 92% in ground Mostly to different habitat type Maximum seed load: 66 trip ⁻¹ Seed caching effort: 520 day ⁻¹	Dominant seed disperser; long-distance disperser; protection from predation; colonization of novel habitat; regeneration of burned area	26
	Mt. Yumori, northern Japan	<i>P. pumila</i>	Seedlings established from caches Cache location: below shrubs	Dominant seed disperser; colonization of novel habitat	27
	Hokkaido, Japan; mixed coniferous forest	<i>P. pumila</i>	Seed caching effort: 294 day ⁻¹ 96% of pine seeds removed (vs. other seed predators) Distance: 100–1,000 m Location: 83% into novel habitat	Dominant seed disperser; long-distance disperser; dispersal into novel habitat	28

TABLE 1. Continued.

Scatter-hoarder	Location and habitat	Tree species	Dispersal parameters	Symbiotic benefit	Reference ^a
Clark's Nutcracker (<i>Nucifraga columbiana</i>)	Arizona, USA; subalpine conifer forest, pinyon- juniper woodland	<i>P. flexilis</i> , <i>P. edulis</i>	Seed selectivity: 4.5% discarded Maximum distance: 22,000 m Minimum distance: 7,500 m Caching location: below/ near other trees Seed caching effort: 200–330 day ⁻¹	Enhanced seed viability; long- distance dispersal; enhanced germination and establishment; dominant seed disperser	29
	California; subalpine conifer forest	<i>P. albicaulis</i>	Maximum distance: 12,500 m	Dominant seed disperser; long- distance disperser	30
	Wyoming, USA; subalpine conifer forest	<i>P. albicaulis</i>	Seed caching effort: maximum 500 hr ⁻¹ Maximum distance: 7,000 m	Dominant seed disperser; long- distance disperser	31
	California, USA; subalpine conifer forest	<i>P. albicaulis</i>	Cache depth: 1–3 cm Caching location: near other trees as well as in burned areas Seed caching effort: 2.6 × the energy needed the following winter	Dominant seed disperser; enhanced germination and seedling establishment; colonization of newly available area; mutualism hypothesis supported	32
	Utah, USA; subalpine conifer forest	<i>P. flexilis</i> , <i>P. edulis</i>	Maximum distance: 5,000 m Seed caching effort: 350 day ⁻¹	Dominant seed disperser; long- distance disperser	33
	Montana, USA; whitebark pine forest	<i>P. albicaulis</i>	Cache location: recently burned or early- succession habitat	Colonization of newly available habitat	34
	Washington, USA; subalpine to alpine conifer forest	<i>P. albicaulis</i> , <i>P.</i> <i>ponderosa</i> , <i>P.</i> <i>Pseudotsuga</i> <i>menziesii</i>	Maximum distance: 29,200 m Average distance: 10,600 m (<i>P. albicaulis</i>)	Dominant seed disperser; long- distance dispersal	35
	Washington, USA; subalpine to alpine conifer forest	<i>Pinus albicaulis</i> , <i>P.</i> <i>ponderosa</i>	Maximum distance: 32,600 m Median distance: 2,100 m (<i>P. ponderosa</i>) Median distance: 5,200 m (<i>P. albicaulis</i>) Location: near understory cover, 42% below ground (<i>P. ponderosa</i>), 15% below ground (<i>P.</i> <i>albicaulis</i>)	Dominant seed disperser; long- distance dispersal; enhanced germination and seedling establishment	36

^a (1) Carmen 2004; (2) DeGange et al. 1989; (3) Pesendorfer 2014; (4) Hubbard and McPherson 1997; (5) Lenda et al. 2012; (6) Culliney et al. 2012; (7) Darley-Hill and Johnson 1981; (8) Johnson and Adkisson 1985; (9) Johnson et al. 1997; (10) Heinrich 2014; (11) Thayer and Vander Wall 2005; (12) Fuchs et al. 2000; (13) Bossema 1979; (14) Kollmann and Schill 1996; (15) Mosandl and Kleinert 1998; (16) Gómez 2003; (17) Stimm and Knoke 2004; (18) Pons and Pausas 2007a; (19) Morán-López et al. 2015a; (20) Balda and Bateman 1971; (21) Ligon 1978; (22) Marzluff and Balda 1992; (23) Stotz and Balda 1995; (24) Holtmeier 1966; (25) Tomback et al. 1993; (26) Hutchins et al. 1996; (27) Kajimoto et al. 1998; (28) Hayashida 2003; (29) Vander Wall and Balda 1977; (30) Tomback 1978; (31) Hutchins and Lanner 1982; (32) Tomback 1982; (33) Vander Wall 1988; (34) Tomback et al. 2001; (35) Lorenz and Sullivan 2009; (36) Lorenz et al. 2011.

Blue Jays showed the same avoidance of large acorns and preferred small acorns from pin and willow oaks. Interestingly, preferred acorns also had higher tannin content (Scarlett and Smith 1991). By contrast, Moore and Swihart (2006) showed, on the basis of experiments with different acorn types, that Blue Jays will eat less-preferred acorns when other options are unavailable; they also found that Blue Jays preferred acorns with lower tannin content when the size was similar and argued that these factors were confounded in other studies. In summary, when multiple species of oaks are present in a community, the effects of the birds' seed selectivity can be positive for trees with preferred seed characteristics, and negative for trees with less-preferred seeds (Lichti et al. 2014).

Seed selectivity by corvids directly results in high seed dispersal quality, but other dispersers are less discriminatory or damage acorns during harvest. Eastern gray squirrels (*Sciurus carolinensis*) readily eat and disperse acorns infested by weevils (Curculionidae), the most common arthropods found in acorns (Steele et al. 1996). Similarly, seed-dispersing rodents in Spanish woodlands exhibited a weak preference for healthy acorns but still dispersed large numbers of acorns with weevil damage or weevils inside (Perea et al. 2012). Some squirrels also prevented germination of acorns by excising the embryo before caching the seeds (Steele et al. 2001). Nevertheless, rodents play an important role in dispersal communities and move large proportions of seeds where they are present (Gómez et al. 2008, Siepielski and Benkman 2008).

Transportation Distance and Frequency

Scatter-hoarding rodents and marsupials are often important dispersers of large seeds in tropical areas, but corvids are the dominant dispersers for large-seeded plants in many northern temperate communities (Table 1; Forget and Vander Wall 2001, Jansen et al. 2004, Russo 2005, Purves et al. 2007, Whelan et al. 2008, García and Martínez 2012). Rodents that compete with birds for seeds rarely disperse them over distances >100 m, but they often dominate local dynamics in those same communities (Howe and Smallwood 1982, Siepielski and Benkman 2007, Gómez et al. 2008). However, there have been few explicit comparisons of different dispersers and their dispersal distances for the same tree (Gómez 2003, Thayer and Vander Wall 2005, Gómez et al. 2008).

After selecting seeds at the tree, corvids transport them in their bill, crop, or sublingual pouch, the latter an adaptation evolved specifically for efficient seed transportation over potentially extensive distances (Bock et al. 1973). Transportation distances can range from a simple hop from the source tree to flights that are tens of kilometers in length (Table 1). Equally important is the fact that seeds are often moved among patches of habitat, differentiating corvids from scatter-hoarding rodents that

rarely cross open patches and generally disperse seeds over shorter distances (Vander Wall 1990).

The longer the maximum dispersal distance by any given vector, the more likely the plants are to benefit from such colonization events (Nathan et al. 2008). North American oaks and beeches, for example, experienced rapid northward range expansion of several hundred meters per year after the Last Glacial Maximum; this was likely driven largely by corvid seed dispersal (Johnson and Webb 1989). As temperature and precipitation patterns change globally, such dispersal will play a crucial role in the ability of plants to shift the altitude and latitude of their ranges (Parmesan 2006, Montoya et al. 2008, Engler and Guisan 2009).

Corvids gather seeds at high rates while they are available and may gather many per visit, depending on seed size. Pinyon Jays (*Gymnorhinus cyanocephalus*), for example, transport ≤ 56 pine seeds visit⁻¹, and nutcrackers regularly cache >500 seeds day⁻¹ (Vander Wall and Balda 1977, Marzluff and Balda 1992, Hutchins et al. 1996). Over a fruiting season, nutcrackers cache tens of thousands of pine seeds, often more than twice as many as necessary to feed them through the subsequent winter (Tomback 1982, 2016, Tomback and Linhart 1990). Acorns are generally not transported in such large numbers, perhaps because they are much larger, but jays can carry as many as 3 at a time and cache $\leq 5,000$ yr⁻¹, often recovering fewer than half of them (Bossema 1979, Darley-Hill and Johnson 1981, DeGange et al. 1989, Gómez 2003, Carmen 2004, Pesendorfer 2014).

Seed Deposition and Directed Dispersal

Corvids store food items by thrusting them into the substrate with their bill, positioning them in a way that they cannot be seen, and covering them with materials from the surrounding area. Depending on the substrate, the item is lodged into a crack or crevice, or the birds use their bill to create the space before placing the food (Brown 1970, Bossema 1979, Vander Wall 1990). The seeds are usually positioned at a depth of 1–5 cm, which inhibits dehydration and often protects them from vertebrate predators (Bossema 1979, Vander Wall and Balda 1981, Tomback 1982, Borchert et al. 1989, Greenberg et al. 2012).

Corvids do not hide seeds with the intention of cultivating seedlings. In some areas, Clark's Nutcrackers cache a majority of pine seeds in areas that are unsuitable for germination, such as tree bark or rock crevices, and only a small proportion is cached in locations that allow seedlings to germinate (Lorenz et al. 2011, Neuschulz et al. 2015). Elsewhere, however, birds place seeds in areas that are well suited for seedling establishment, and most other corvids hide a majority of items in the ground, where germination is possible (Vander Wall 1990, Tomback et al.

2001). This positioning of a large number of seeds in safe sites is one of the unique aspects of scatter-hoarding seed dispersers (Vander Wall and Beck 2012).

Directed dispersal occurs when seeds are placed in areas that favor germination and seedling establishment. This behavior is performed by a considerable number of corvids and provides an important advantage in the first steps of establishment (Johnson et al. 1997, Wenny and Levey 1998, Wenny 2001, Whelan et al. 2008). In habitat degraded by human activity and drought in the Mediterranean Basin, animal-dispersed trees exhibit stronger resilience to habitat fragmentation and destruction than wind-dispersed species; this effect is likely a consequence of long-distance seed dispersal, as well as of directed dispersal to areas with increased likelihood of seedling establishment and survival (Montoya et al. 2008). Corvid-mediated seed dispersal can thus have profound effects on the community structure of the patch in which seeds have been placed (Johnson et al. 1997, Culliney et al. 2012, Lenda et al. 2012).

Both Old World and New World jays perform directed dispersal by hiding seeds below other plants, at the transition zone between vegetation types, or in recently disturbed areas (Bossema 1979, Tomback 1982, Borchert et al. 1989, Lenda et al. 2012). For seeds and seedlings, such areas can serve as nurse environments by reducing water stress and ungulate herbivory (Callaway and D'Antonio 1991, Broncano et al. 1998, Leiva et al. 2013). In North America, for example, several species of corvids frequently cache in recently burned or disturbed areas, allowing oaks and pines to colonize newly available habitat (Johnson et al. 1997, Lenda et al. 2012). In Spanish woodlands and managed (agroforestry) *dehesas*, oak seedling recruitment is limited to areas with oak canopy cover and to years with increased precipitation (Mendoza et al. 2009). Fifty percent of holly oak (*Q. ilex*) acorns planted below shrubs to mimic jay caches survived 8 mo as seedlings, whereas only 16% of acorns planted in the open or below artificial shade survived over that time (Smit et al. 2008). The degree of directed dispersal can vary strongly with habitat. Morán-López et al. (2015a) showed that acorns harvested in oak forests are more likely to arrive in suitable habitat than acorns from *dehesas*. The topic of context dependence of directed dispersal by corvids thus requires more research.

Masting: Seed Dispersal Insurance for Oaks and Pines?

Many large-seeded trees dispersed by scatter-hoarders have spatially synchronized seed production with cyclical bumper crops, a phenomenon termed “masting” or “mast-fruited” (Koenig and Knops 2000). Masting appears to be an evolved strategy that interacts with environmental factors to produce synchronous bumper crops over large

geographic areas that can be hundreds or thousands of square kilometers in size (Kelly and Sork 2000, Koenig et al. 2003, Koenig and Knops 2013). Masting leads to strong temporal pulses in resources, which reverberate through the whole ecosystem (Ostfeld and Keesing 2000). Seed predators and dispersers such as insects, rodents, and birds respond functionally to mast years with increased reproductive success (Ostfeld and Keesing 2000, Espelta et al. 2009, Koenig et al. 2009). The effect of masting on the scatter-hoarding behavior of corvids, however, is not fully understood.

Two non-mutually exclusive hypotheses make predictions about the effect of masting on seed fate. The “predator satiation hypothesis,” arguably the best-established hypothesis for the functional significance of masting, proposes that seed consumer populations are overwhelmed in bumper crop years, resulting in a larger proportion of seeds that survive until reproduction (Kelly and Sork 2002). This hypothesis, however, makes no clear predictions about the dispersal of the surviving seeds. The “predator [or animal] dispersal hypothesis” proposes that, in addition to predator satiation, mast years improve seed dispersal benefits that plants receive from scatter-hoarders (Vander Wall 2002, 2010). The latter hypothesis is still controversial, and the details of how seed dispersal is affected by masting need to be addressed in future research.

Evidence supporting the predator dispersal hypothesis as a selective advantage of masting mostly comes from rodents. Red acouchis (*Myoprocta acouchy*), medium-sized rodents that scatter-hoard seeds of *Carapa procera*, a large-seeded rainforest tree, increased seed dispersal effectiveness in years of bumper crops by increasing seed removal rates and distances, as well as by hoarding larger seeds that were more likely to germinate (Jansen et al. 2004). Jeffrey pines (*P. jeffreyi*), dispersed by multiple rodent species, experienced seed removal rates that were 4–8 times faster and dispersal distances that were ~25% farther in mast years than in a regular crop year (Vander Wall 2002). While the increase in dispersal rates in mast years may be explained by a functional or numerical response of foraging animals to seed availability, the mechanisms that lead to increased dispersal distances are unclear (Vander Wall 2002, 2010). Bumper crops can also increase plant fitness by affecting other dispersal parameters. Rodents dispersing *Prunus armeniaca* in China, for example, increased the proportion of seeds that were scatter-hoarded rather than placed in a single larder during a mast year (Li and Zhang 2007). Masting can therefore function to ensure high-quality seed dispersal by increasing the mutualistic benefit the trees receive from scatter-hoarding rodents (Vander Wall 2010).

Bumper crops may affect scatter-hoarding in corvids in ways similar to the effect on rodents, but few studies have

addressed this issue. Johnson et al. (1997) noted that scatter-hoarding rates by Blue Jays were significantly reduced in a year of low crop production. Similarly, dispersal rates and distances of acorns scatter-hoarded by Island Scrub-Jays (*Aphelocoma insularis*) were positively correlated with acorn crop size in local oaks (Pesendorfer 2014). Finally, Siepielski and Benkman (2008) demonstrated that Clark's Nutcrackers showed greater selectivity among trees during bumper crop years. Given that these birds tend to prefer trees with large individual crops of sizable, healthy seeds (Christensen et al. 1991), this may also affect the fitness benefits that the trees receive from seed dispersal. Although the response of scatter-hoarding by corvids to masting of trees still requires more research, its role as a long-distance dispersal mechanism that enables plants to colonize new habitat and change ecosystem dynamics is well established.

Dispersal, Colonization, and Ecosystem Engineering

Bird dispersal of seeds is often a major driver of vegetation succession and land reclamation after disturbance. If the area surrounding the disturbed site provides enough bird habitat and seeds to disperse, birds will accelerate plant succession on disturbed patches (Robinson and Handel 1993, 2000, Neilan et al. 2006, Howe and Martínez-Garza 2014). Directed dispersal by corvids can have large-scale effects on the geographic expansion and resilience of tree populations and their associated ecosystems (Lankau et al. 2011). Driven by long-distance seed dispersal, tree populations can quickly respond to changes in climate and habitat availability despite the immobility of the adult plants (Johnson and Webb 1989, Kollmann and Schill 1996). For example, old fields in Poland were quickly colonized by black walnuts (*Juglans regia*) because Rooks (*Corvus frugilegus*) and Carrion Crows (*C. corone*) preferentially cached nuts in such disturbance zones. Consequently, the range of *J. regia* has undergone rapid expansion over the past 50 yr in this region (Lenda et al. 2012).

Colonization of new areas by oaks and pines not only changes the species interactions in a patch; it also changes the concentrations of carbon, nitrogen, and soil nutrients as well as soil moisture retention and other abiotic conditions (for a broader discussion of oak effects on ecosystems, see Campos et al. 2013). Oak and pine trees create "fertility islands" through organic-matter incorporation and nutrient cycling. Soils beneath the canopy have lower bulk density, higher pH, and greater concentrations of organic carbon, nitrogen, and total and available phosphorus than soils of neighboring grassland (Dahlgren et al. 1997, Quideau et al. 1998, 2001). Oaks in Texas savannas ameliorate conditions for shrubby plants, initially favoring their establishment by providing shade, but potentially limiting their access to water as the understory plants increase in size (Anderson et al. 2001). Forest

patches can expand by facilitating establishment of understory shrubs and conspecifics that are competing with surrounding grasses. Increased shade, water, and soil nitrogen availability allow trees to become established at the edge of forest fragments, creating a positive feedback loop (Li and Wilson 1998).

Such engineering is central to ecosystem restoration because it provides long-lasting changes that extend beyond an individual plant's area and life span (Byers et al. 2006, Crain and Bertness 2006, Hastings et al. 2007). As keystone hardwood species, oaks are major drivers of biodiversity and affect abiotic variables over extended periods (McShea and Healy 2003, Johnson et al. 2009). Similarly, pines change the soil chemistry of patches and facilitate establishment of understory plants in alpine and subalpine habitats (Quideau et al. 1998, Baumeister and Callaway 2006). In coastal California, tall vegetation such as oaks and pines captures moisture from fog, producing an important water input into the ecosystem (Dawson 1998, Fischer et al. 2009). Establishment and expansion of oak and pine stands can thus change the resource availability of the surrounding environment, which can facilitate the subsequent arrival of other plants and animals. This process is often enabled by long-distance seed dispersal by corvids, which suggests that the impact of the birds as a dispersal vector can affect the dynamics of whole ecosystems (see Tomback 2016).

Below, we provide examples of the mutualism between corvids and oak or pine trees that span different habitat types and broad geographic regions (Table 1 and Figure 2). We also highlight case studies of how corvid scatter-hoarding behavior can be utilized in habitat restoration efforts. The value of ecosystem services provided by birds is increasingly recognized and can provide a cost-effective enhancement or alternative to existing restoration methods (Whelan et al. 2008, Wenny et al. 2011).

MUTUALISMS AROUND THE NORTHERN HEMISPHERE

Eurasian Jays and Oaks

Eurasian Jays (*Garrulus glandarius*) are associated with oak and pine habitat throughout their range, extending from England to Japan (Figure 2). These birds eat acorns, fruits, invertebrates, and vertebrates, and store acorns throughout the fall (Bossema 1979). The jays are selective between acorns of different species and sizes, preferentially selecting larger acorns unless they are too large for their gape (Pons and Pausas 2007b). Acorns are dispersed as long as they are available, even when presented out of season (Pons and Pausas 2007a).

In heterogeneous landscapes, Eurasian Jays disperse seeds unevenly among available habitat (Morán-López et al. 2015a). Because the birds have strong habitat preferences, habitat composition affects the spatial distribution

of caches (Pons and Pausas 2007a); they disproportionately cache seeds in disturbed areas such as recently abandoned fields and roadside areas, but also in mowed grass (Kollmann and Schill 1996), in the transition zone between vegetation types (Bossema 1979), and in areas with low densities of oaks (Gómez 2003). These are often the microhabitats that favor oak recruitment and yield the highest seedling densities (Pausas et al. 2004, Pons and Pausas 2007a). Habitat preferences, both when foraging and caching, can vary significantly between managed areas, such as *dehesas*, and continuous forest. Morán-López et al. (2015a) recently demonstrated that acorns from *dehesa* oaks are less likely to be cached in ways that promote recruitment than acorns from oak forests.

Eurasian Jays are the predominant dispersers of acorns over large distances (Perea et al. 2011), but other animals, such as wood mice (*Apodemus* spp.), red squirrels (*S. vulgaris*), and even dung beetles (*Thorectes lusitanicus*) also cache acorns (den Ouden et al. 2005, Gómez et al. 2008, Pérez-Ramos et al. 2013, Morán-López et al. 2015b). Rodent dispersal plays an important role in within-patch dynamics, but rodents often hesitate to cross open spaces. In fragmented, heterogeneous landscapes, model simulations of oak woodland dynamics in Spain suggest that directed dispersal by jays enhances regional abundance of large-seeded trees (Purves et al. 2007). In fact, jay-dispersed plants show stronger resilience in the face of habitat destruction and fragmentation than other plants that are dispersed by wind (Montoya et al. 2008). Thus, as habitat fragmentation and climate change affect European hardwoods, Eurasian Jays are likely to be an increasingly valuable ally for the oaks (Montoya and Raffaelli 2010).

While much is known about the role of Eurasian Jays as oak dispersers in Western and Central Europe, little is known about European Jay dispersal of oaks and other plant species over most of the jay's range (Figure 2). Because seed dispersal dynamics and scatter-hoarding by corvids are highly context dependent, more research is needed to explore the generality of the ecological role of Eurasian Jays in oak woodland dynamics.

Nutcrackers and Pines

Nutcrackers (Europe: *N. caryocatactes*; North America: *N. columbiana*), renowned scatter-hoarders that spend a majority of the fall harvesting and caching pine seeds, carry as many as 150 pine seeds at a time in their sublingual pouch (Bock et al. 1973, Tomback 1978). Nutcrackers transport seeds as far as 32 km and place them in caches of 1–15 seeds (Vander Wall and Balda 1977, 1981, Tomback 1978, 1982, Lorenz et al. 2008, 2011). As a consequence, nutcracker-dispersed pines in the Old World and the New World regularly show a “tree cluster” or “multi-genet” growth form that consists of genetically

different individuals (Tomback and Linhart 1990, Tomback et al. 1993, 2001, Tomback 2005).

Lesser and Jackson (2013) showed that repeated long-distance dispersal events by nutcrackers were necessary to establish and stabilize a population of ponderosa pines in the Rocky Mountains, USA. Various substrates and habitats serve as cache locations, ranging from leaf litter in closed-canopy forests to rock crevices and the bark of other pine trees (Lorenz et al. 2011). When placed in the ground, nutcracker caches are usually found 2.5 cm below the surface, an optimal depth for pine seed germination (Tomback 1982). Clearly, not all cache sites are suitable for seed germination and recruitment by pines, but the sheer number and distribution of dispersed seeds across the landscape enables trees to colonize new habitats, providing the trees with mutualistic benefits (Tomback et al. 2001).

In the fall, nutcrackers often fly to lower elevations to gather pine seeds that are then transported back to their territories. Nutcrackers therefore have a strong influence on pine population structure and may allow the plants to track elevational shifts of suitable habitat as the climate changes (Richardson et al. 2002, Tomback 2005, Lesser and Jackson 2013). The birds also exert selection on pine characteristics, choosing pines with more rewarding cones and larger seeds (Siepielski and Benkman 2008). A fifth of all pines—species whose seeds have lost their wings—rely on this mutualism as their dispersal mode (Tomback and Linhart 1990).

Other plant species benefit from this keystone mutualism. Pines ameliorate harsh environmental conditions by changing abiotic factors, such as soil moisture and temperature, as well as exposure to wind and sun. On harsh sites, nutcracker-dispersed pines often act as nurse trees for seedlings of some shrubs and trees (Callaway 1998, Baumeister and Callaway 2006). Nutcrackers disperse whitebark pine seeds to the treeline; there, dwarfed (krummholz) whitebark pines may act as nurse trees, leading to the formation of tree-island conifer communities (Resler and Tomback 2008, Tomback 2016).

New World Jays, Oaks, and Pines

North and South America are home to a diverse group of jays, the New World jays. While little is known about the scatter-hoarding of Neotropical jay taxa, the behavior of temperate North American jays is comparatively well studied. These birds are associated with oak or pine habitat throughout their range (Figure 2) and typically scatter-hoard seeds (Pitelka 1951, Vander Wall 1990, Peterson 1993). An exception is the Gray Jay (*Perisoreus canadensis*), a sister group to the Old World Siberian Jay (*P. infaustus*) found throughout Canada and in alpine areas of the United States, which occasionally scatter-wards seeds but mostly stores arthropods, berries, and

fungi in aboveground caches along tree trunks (Waite 1988).

Pinyon Jays are strong fliers and cache seeds as far as 11 km from their harvest location (Vander Wall and Balda 1981, Marzluff and Balda 1992). This long-distance dispersal likely contributes to high levels of heterozygosity in pockets of twoneedle pinyon (*Pinus edulis*) woodland at the northern edge of the tree's distribution, contrasting with the homozygosity indicative of founder effects common to peripheral stands of many other tree species (Betancourt et al. 1991). This points to repeated dispersal into the area, likely due to Pinyon Jay and nutcracker caches placed there over the past 500–1,000 yr. Seed dispersal activity by Pinyon Jays has probably not only expanded the range of pinyon pines, but also helped maintain pine genetic diversity and population health.

Individual Florida Scrub-Jays (*Aphelocoma coerulescens*), Western Scrub-Jays (*A. californica*), and Island Scrub-Jays (*A. insularis*) cache 5,000–6,000 acorns yr⁻¹ when the acorn crop is good and have been shown to enhance oak habitat recovery (DeGange et al. 1989, Carmen 2004, Pesendorfer 2014). For example, blue oak (*Q. douglasii*) acorns that were manually planted to mimic caches created by scrub-jays were twice as successful in establishing seedlings as acorns simply placed on the surface, even when ungulates were excluded. The effect was even stronger in areas exposed to seedling predators (Borchert et al. 1989). *Aphelocoma* caching behavior also contributes to postfire habitat recovery because their ground caches are likely to survive the high temperatures and the acorns face little competition when sprouting after fire (Pase 1969, Borchert et al. 2003, Borchert and Tyler 2010). Despite an abundance of research on scatter-hoarding by *Aphelocoma*, however, comparatively little is known about their role as seed dispersers.

Blue Jays forage on most oak species in their range, where they are the dominant avian dispersers of acorns (Johnson and Webb 1989, Johnson et al. 1997). In a single fruiting season, Blue Jays collectively transported >130,000 acorns from a stand of 11 pin oaks and 91% of the observed caches were placed in areas suitable for germination, thus promoting colonization of new habitat by the oaks (Darley-Hill and Johnson 1981). Blue Jays increase their caching effort after fires and tend to select canopy gaps and habitat transition zones as their caching sites; these areas also have the most oak seedlings (Johnson et al. 1997). Most remarkable, though, are the distances over which acorns are transported by Blue Jays: up to 4 km, with averages around 1 km (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985, Johnson et al. 1997). In addition to acorns, Blue Jays also disperse the seeds of beeches (*Fagus* spp.) and American chestnut (*Castanea dentata*) (Johnson and Adkisson 1985, Heinrich 2014). The combination of intense harvesting effort and cache

placement highlights the role of these corvids as a keystone species in the life history of many oaks in eastern North America.

CORVID SEED DISPERSAL AND HABITAT RESTORATION

Oak and pine habitats are being degraded and/or managed as working landscapes throughout the Northern Hemisphere (Thomas et al. 2002, Abrams 2003, Wang et al. 2007, Campos et al. 2013). These declines are driven by a variety of factors, ranging from climatic conditions that affect forest health to heightened vulnerability to catastrophic wildfire caused by forest management practices (Odion and Hanson 2006). Browsing by ungulates (MacDougall 2008) and competition with introduced grasses also reduce recruitment (MacDougall et al. 2010). Shifts in rainfall and temperature patterns have been correlated with an increase in damage by fungal pathogens (Rizzo and Garbelotto 2003, Tomback and Achuff 2010) and arthropod pests (Coleman and Seybold 2008, Kurz et al. 2008). Rapid climate change could also cause the environmental conditions suitable for oaks and pines to shift on a large scale (McKenney et al. 2007); thus, long-distance seed dispersal and subsequent ecosystem engineering processes could be crucial to the ability of oak and pine ecosystems to respond accordingly (Johst et al. 2002, Thuiller et al. 2005, Trakhtenbrot et al. 2005, Montoya et al. 2008, McConkey et al. 2012).

On a shorter time-scale, seed dispersal by scatter-hoarding corvids can provide valuable ecosystem services in the context of maintaining or restoring pine and oak habitat (Şekercioğlu et al. 2004, Wenny et al. 2011). The role of seed dispersal as an ecosystem service with tangible benefits for humans is becoming broadly recognized and has recently been highlighted in the scientific literature (Whelan et al. 2008, Wenny et al. 2011). Independently, managers have identified the use of seed dispersers and ecosystem engineers as a particularly cost-effective and efficient way to restore habitat (Byers et al. 2006, de la Peña-Domene et al. 2014, Howe and Martínez-Garza 2014). By manipulating corvids into providing seed dispersal in targeted areas, or by creating conditions under which the dispersed seeds can contribute to regeneration, managers can utilize the birds' behavior to achieve conservation goals.

Oak Woodland Restoration in Western Europe

Land managers in Western Europe have long recognized the role of seed dispersal by Eurasian Jays in maintaining and restoring oak habitat. Although many foresters considered corvids a pest that steal valuable acorn crops and kill other passerines, early discussions in forestry journals reveal that they also recognized their contribution

to oak regeneration (Stimm and Knoke 2004, Madden et al. 2015). For example, Krebs (1889) wrote that “It is unnecessary to seed oaks, because the jays do so in abundance” (translated from German). Similarly, Stimm and Knoke (2004) cited examples dating back as far as 1653 in which poets described the hoarding activity of the birds, as well as the positive impact on oak regeneration.

German foresters are actively taking advantage of the ecosystem services provided by jays. In an approach termed “ecological silviculture,” large old oaks that serve as a seed source are conserved and wooded areas are thinned to increase oak seedling growth. Mosandl and Kleinert (1998) estimated the contribution of jays as amounting to 2,000–4,000 young oaks ha⁻¹ in an eastern German forest. If seed crops are low, large baskets of seeds are offered, and, in combination with the exclusion of seedling predators, such as “jay-oaks” (German *Hähereichen*) can contribute significantly to the profitability of forested lands (Stimm and Knoke 2004).

Restoration efforts can also profit by saving on the costs of planting trees in public space. For an urban forest in Stockholm, Sweden, Hougner et al. (2006) calculated that replacing “planting” efforts performed yearly by Eurasian Jays with human labor would cost \$2 acorn⁻¹, or as much as \$9,400 ha⁻¹ of forest annually. A fraction of such replacement costs could be invested in maintaining or creating optimal jay habitat, resulting in similar forest maintenance. In Spain, managers tasked with oak habitat restoration plant small areas of seed-source trees that attract scatter-hoarders to deposit caches at the edge of the vegetation (Rey Benayas et al. 2008). This habitat-islet strategy has been successfully applied to Mediterranean old fields as a cost-effective alternative between full afforestation and simple abandonment of agricultural fields (Rey Benayas and Bullock 2012). An analysis of jay nesting and habitat use pattern also suggests that clearing of brush and maintenance of diverse and complex habitat structure may increase jay densities and consequent oak restoration (Pons and Pausas 2008). More recently, however, Morán-López et al. (2015a) demonstrated that the jays’ hoarding behavior can vary tremendously between continuous forest and *dehesas*. Dispersal rates, distances, and habitat selectivity all varied between the 2 habitat types, illustrating that the birds prefer to forage on and cache acorns from forest trees, and that those acorns are also cached in ways that are more likely to result in oak regeneration, than is the case for acorns from *dehesas* (Morán-López et al. 2015a). Restoration strategies thus need to be adjusted to site-specific needs in order to maximize the ecosystem services provided by the birds.

Still, many corvids are culled regularly under the assumption that they are only a crop pest and significantly reduce populations of other passerines. A recent analysis, however, revealed that such detrimental impacts are often

minute at worst (Madden et al. 2015). Stimm and Böswald (1994) therefore made a strong argument against the culling of corvids, especially Eurasian Jays, by highlighting their useful attributes, such as the silvicultural and restoration benefits described above. Supplementing acorns, maintaining jay-friendly habitat, and restricting jay hunting within target areas can thus positively affect oak habitat restoration.

Whitebark Pine Restoration in the Rocky Mountains

Whitebark pine, a keystone species in the Rocky Mountains of western North America (Tomback 2005), has declined throughout its range as a result of blister rust infestation, mountain pine beetle (*Dendroctonus ponderosae*) attacks, and fire suppression (Tomback et al. 2001, Scott and McCaughey 2006, Tomback and Achuff 2010). Clark’s Nutcrackers are the main seed dispersers of whitebark pine (*P. albicaulis*; Tomback 1982), and they forage less frequently in trees that have reduced cone crops due to tree damage and mortality by blister rust and bark beetles. In fact, cone abundance thresholds identified for nutcracker foraging are now used to categorize areas for restoration efforts (McKinney and Tomback 2007, McKinney et al. 2009, Barringer et al. 2012).

Managers use multiple methods to enhance the nutcracker–pine mutualism. Catering to nutcracker caching preference, suitable areas have been created by prescribed fire and silvicultural practices (Keane and Parsons 2010). Such areas attract nutcracker caching but, for unknown reasons, have resulted in little regeneration of pines. Meanwhile, other areas may comprise trees that are resistant to the fungal infestation that causes blister rust. Consequently, recovery plans also include the propagation of seed from resistant trees in areas that are still largely intact (Schoettle and Sniezko 2007); but in highly degraded areas, different tactics are necessary (Tomback and Achuff 2010, Tomback 2016). Combined with site preparation to enhance survival of seedlings and young trees, managers could take advantage of seed dispersal by nutcrackers to distribute seeds of resistant trees throughout the landscape.

Recovery of Oak Chaparral and Pine Woodland in Channel Islands National Park

Oak and pine vegetation on the 2 largest islands, Santa Cruz and Santa Rosa, in southern California’s Channel Islands National Park are recovering from 150 yr of grazing by introduced livestock (Van Vuren and Coblentz 1987, Morrison 2011). The extent of these habitats on Santa Cruz Island has more than doubled since livestock removal began in the late 1980s, likely aided by the endemic Island Scrub-Jay (Morrison et al. 2011). Furthermore, the spatial patterns of vegetation expansion suggest that Island Scrub-Jay seed dispersal was an important driver of the island’s

TABLE 2. Summary of hypotheses addressing the interactions of corvid and plant behavior.

Impact level	Hypothesis	Support
Seed selection	Positive effect on dispersal quality by avoiding parasitized or damaged seeds	Strong
Dispersal distance	Generally longest dispersal distance among disperser communities	Strong
Habitat selectivity	Habitat preferences during caching lead to directed dispersal	Moderate
Deposition in microhabitat	Species that cache seeds in ground place them in optimal position for germination while reducing probability of secondary predation and desiccation	Moderate
Gene flow	Dominant long-distance seed disperser, especially in heterogeneous landscapes	Strong
Range expansion and colonization	Long dispersal distances combined with habitat preferences for disturbed areas and/or edges of potential nursing plants	Moderate
Ecosystem engineering	Corvid-dispersed plants permanently change abiotic and biotic parameters of patch	Weak
Masting affects seed dispersal	Temporal variation in seed production affects dispersal parameters	Weak

passive recovery (Beltran et al. 2014, Dahlin et al. 2014). This corvid is one of the rarest and most range-restricted passerine species in the United States, with an estimated total population of <3,000 individuals (Sillett et al. 2012). Nonetheless, because each individual jay is estimated to disperse $\sim 4,500$ acorns yr^{-1} , this population may transport ~ 7 million acorns yr^{-1} (Pesendorfer 2014). On Santa Rosa Island, which lacks Island Scrub-Jays, the recovery of oak and pine habitats has been slow. Oaks and pines experienced little apparent recruitment until nonnative ungulates were fully eradicated in 2011.

Restoration of oak and pine habitats on Santa Rosa Island, in the absence of a scatter-hoarding jay, will require either an enormous investment of capital and human labor or many decades to centuries of time. Island Scrub-Jays, however, formerly occurred on Santa Rosa Island, perhaps into the 19th-century ranching era (Collins 2009). Translocation of Island Scrub-Jays to Santa Rosa Island is a potential strategy to both abate threats associated with the jays' small population size and restricted range and accelerate restoration of the island's oak and pine habitats (Morrison et al. 2011). Island Scrub-Jays would likely rapidly disperse Santa Rosa Island's oaks (*Q. pacifica*, *Q. agrifolia*, and *Q. tomentella*) and Bishop pines (*P. muricata*), as well as seeds from the small endemic population of Torrey pine (*P. torreyana*), a range-restricted species that, like the jay, is considered vulnerable (IUCN 2012). Both the island endemic jay and its mutualistic partners could benefit from proactive conservation action while providing a cost-effective alternative to human labor (Hougner et al. 2006, Morrison et al. 2011).

CONCLUSIONS

Grinnell's (1936) observations of the mutualistic benefits that large-seeded trees gain from scatter-hoarding birds are now supported by a large body of scientific literature.

Corvids that live in close relationships with pines and oaks are often the dominant seed disperser with high dispersal effectiveness; they prefer to gather viable seeds, transport them over long distances, and place many of them in locations favorable for their establishment. As a result, these large sessile plants have proved quite mobile when colonizing new habitat or responding to environmental change (Table 2). Although our understanding of these birds' seed dispersal effectiveness has increased substantially, additional research is needed on the role of seed dispersal distance in providing fitness benefits to plants.

As trees are pressed to track increasing temperatures northward or to higher elevations, long-distance dispersal through heterogeneous landscapes is likely to increase in importance. Models of contemporary and historical population dynamics of oaks and other large-seeded trees suggest that corvid seed dispersal plays a pivotal role in the ability of populations to maintain and shift their range (Johnson and Webb 1989, Purves et al. 2007, Montoya et al. 2008). In areas where seed dispersal has recently stalled because of the near extinction of a local corvid, regeneration and spatial spread of large-seeded plants has been limited (Culliney et al. 2012). The mobility that corvid seed dispersers provide to sessile plants will likely be central to the response to large-scale shifts in climatic patterns. However, the potential effects of climatic shifts on complex species interactions, such as seed dispersal mutualisms, are still poorly understood (Cairns et al. 2007, Walther 2010).

The importance of the seed dispersal mutualism between corvids and large-seeded trees for species of conservation concern emphasizes the need to improve our understanding of management opportunities, including the use of ecosystem services by corvids. In many areas of the Northern Hemisphere, oak and pine habitats are declining and, because of their role as keystone species for

whole ecosystems, are becoming the focus of restoration efforts. Some techniques, such as seed addition, the creation of space that jays use for caching, and the creation of habitat islets as a seed source, have long been used by foresters and managers. Nonetheless, we believe that there is greater potential for the use of corvid ecosystem services and engineering in the habitat maintenance and restoration context. Future work should thus determine the conditions that enhance seed dispersal both in time and space, examine the balance between seed predation and dispersal, and further assess the geographic extent of the interaction between birds and trees. This effort would further elucidate the ecological and evolutionary implications of bird–plant interactions and provide a promising way forward in modern, cost-effective conservation.

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