

SYNTHESIS & INTEGRATION

The ecological significance of secondary seed dispersal by carnivores

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Abstract. Animals play an important role in the seed dispersal of many plants. It is increasingly recognized, however, that the actions of a single disperser rarely determine a seed's fate and final location; rather, multiple abiotic or animal dispersal vectors are involved. Some carnivores act as secondary dispersers by preying on primary seed dispersers or seed predators, inadvertently consuming seeds contained in their prey's digestive tracts and later depositing viable seeds, a process known as diploendozoochory. Carnivores occupy an array of ecological niches and thus range broadly on the landscape. Consequently, secondary seed dispersal by carnivores could have important consequences for plant dispersal outcomes, with implications for ecosystem functioning under a changing climate and across disturbed landscapes where dispersal may be otherwise limited. For example, trophic downgrading through the loss of carnivores may reduce or eliminate diploendozoochory and thus compromise population connectivity for lower trophic levels. We review the literature on diploendozoochory and conclude that the ecological impact of a secondary vs. primary seed disperser depends on the relative dispersal distances, germination success, and the proportion of seeds exposed to secondary dispersal by carnivores. None of the studies up to present day have been able to rigorously assess the ecological significance of this process. We provide a framework of the components that determine the significance of diploendozoochory across systems and identify the components that must be addressed in future studies attempting to assess the ecological importance of diploendozoochory.

Key words: climate change; diplochory; diploendozoochory; fragmentation; indirect dispersal; invasive species; polychory; predator; secondary dispersal; seed dispersal; seed dispersal effectiveness; seed predation.

Received 19 December 2016; accepted 22 December 2016. Corresponding Editor: Debra P. C. Peters. Copyright: © 2017 Hämäläinen et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. † E-mail: anni.m.hamalainen@gmail.com

INTRODUCTION

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Owing to their sessile adult lives, plants have evolved numerous ways to ensure offspring disperse away from the immediate vicinity of the parent plant, typically via the movement of seeds. This movement is beneficial because seedlings that take root further away from their parent plant avoid competing with related individuals for resources, reduce density-dependent seedling mortality, and may have better chances of encountering suitable microhabitats for recruitment (Howe and Smallwood 1982). In addition to dispersal by abiotic means such as wind and water, seed dispersal by animals (zoochory) is a common dispersal mechanism that allows seeds to be deposited some distance away from the parent plant through animal vectors. While plants with high rates of seed predation have evolved adaptations that minimize seed losses by animals (Hulme and Benkman 2002), plants that rely on zoochory often produce seeds encased in fleshy fruits to promote consumption by dispersers (endozoochory; Schaefer and Ruxton 2011). Estimates of the number of plants dispersed by animals vary widely, but endozoochory is estimated to be the primary dispersal mechanism in up to 94% of woody plants, depending on the region (Jordano 2000, Buitrón-Jurado and Ramírez 2014). Furthermore, many plants that do not seem to have adaptations for endozoochory can, nevertheless, be dispersed by animals in addition to dispersal by other means such as wind, water, or gravity (Pakeman et al. 2002, Orłowski et al. 2016).

Despite such adaptations, there is increasing evidence that the final fate of seeds is not necessarily determined by the animals that remove them from the parent plant. Instead, multiple dispersal vectors may be involved in taking seeds to their final destination or destruction (Ozinga et al. 2004, Vander Wall and Longland 2004); at the community level, plants were estimated to have on average 2.15 dispersal vectors per species among Dutch ecosystems (Ozinga et al. 2004). There has been increasing interest in diplochory (two-phase dispersal, also known as "secondary dispersal" or "indirect dispersal") involving a second dispersal phase by ants, dung beetles, or scatter-hoarding rodents that physically carry the seeds to a new location (Vander Wall and Longland 2004), but relatively little attention has been paid to "diploendozoochory," that is, seed dispersal that involves the ingestion of the seed by two or more separate species of animals in sequence. Typically, this occurs when a carnivorous predator (hereafter referred to as carnivores) consumes a primary disperser or a seed predator, along with seeds in its prey's digestive tract, and subsequently deposits the seeds in feces or in regurgitated pellets (Dean and Milton 1988, Nogales et al. 2007, 2012). Diploendozoochory was first documented by Darwin (1859), and opportunistic observations have since then been infrequently reported. Although diploendozoochory has recently been approached more rigorously using experiments (Nogales 1999, Nogales et al. 2007, Padilla and Nogales 2009, Padilla et al. 2012), the broader ecological significance of this phenomenon remains largely unknown as few attempts have thus far been made to sufficiently establish the importance of the mechanism. A synthesis of the topic is therefore needed to enable broader predictions on the prevalence and ecological role of diploendozoochory to help direct future research into the phenomenon.

Presumably, the effects of secondary dispersal depend strongly on the characteristics of the animal vectors and plants involved, as well as the habitats they occupy. Therefore, we identified characteristics of the dispersal process that are likely to influence plant fitness via germination or recruitment success and access to suitable habitat. Using this information, we devised a framework to assess the importance of diploendozoochory in plant dispersal success under different conditions. Using this framework, we identified potential ecological consequences of secondary dispersal for ecosystem functioning. We then reviewed the existing literature on the role of carnivores in multi-stage seed dispersal to assess the evidence in support of the identified mechanisms and their implications for plant dispersal.

What Makes Diploendozoochory an Ecologically Significant Seed Dispersal Mechanism?

The overall impact of the dispersal mechanism on plant fitness is composed of the quantity of seeds processed by each dispersal vector, the viability of the seeds after handling and consumption by each disperser, and the likelihood that the dispersed seeds will germinate and mature into reproductive adult plants where they are deposited (seed dispersal effectiveness framework; Schupp and Jordano 2010). In general, a prerequisite for successful endozoochory is that the digestive process of the animal vector does not damage the seed; thus, seeds should be swallowed whole. Furthermore, the viable seed must be deposited by the final disperser at a site that meets the minimum requirements for successful germination: Deposition in a cave or a building (Dean and Milton 1988), a highway or the ocean, will usually impede seed germination.

For a carnivore to improve seed dispersal outcomes, the seed dispersal effectiveness of diploendozoochory must naturally be higher than that of dispersal by a single vector (Schupp and Jordano

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2010). The types of plants and the primary and secondary dispersers involved all influence dispersal effectiveness and the ecological significance of the secondary dispersal phase, as detailed in the framework in Table 1. The involvement of a carnivore in the second phase of the seed dispersal process can influence plant fitness in three ways: by transporting seeds, by altering the viability of transported seeds, and by changing the quantity of seeds that are dispersed.

Long-distance dispersal

Long-distance dispersal in plants, although rare (Cain et al. 2000, Nathan et al. 2008), increases the rate of spread and colonization of new areas (Higgins and Richardson 1999, Lesser and Jackson 2013), with effects on plant population dynamics (Cain et al. 2000, Nathan et al. 2008, Caughlin and Ferguson 2013). As carnivores tend to range much farther than frugivores or herbivores (Carbone et al. 2005), the dispersal distance and deposition site (i.e., location at which the seed ends up after being processed by a disperser, typically within feces or within regurgitated pellets) may differ dramatically for seeds deposited by primary vs. secondary dispersers (Dean and Milton 1988, Nogales et al. 2007, 2012). Secondary dispersal can thus contribute significantly to plant dispersal range and population dynamics, especially when the primary disperser has a relatively small home range size, is movement-restricted, or a habitat specialist (Higgins and Richardson 1999, Nogales et al. 2012). For example, after consuming a prey item with a very small home range (such as a small rodent), a raptor pellet may take up to 22 h to form. During a migration, a bird can cover 480 km in that time (Balgooyen and Moe 1973); this distance could be even longer as some seeds can germinate after a retention time of up to 62 h in birds of prey (Darwin 1859).

Secondary dispersal by far-ranging carnivores can thus enable colonization of newly suitable habitats under climate change or remote areas such as islands (Nogales et al. 2012), or may locally influence the number of seeds entering the seed pool. An increase in dispersal distance may, however, reduce the dispersal success of rare, or habitat-specialist species (Herrmann et al. 2016), unless the dispersers have similar, specialized habitat requirements as the plant. Secondary dispersers may thus deposit seeds in maladaptive locations or out of their climate zone, but the plant could, nevertheless, benefit from the longdistance dispersal if novel, suitable patches are even occasionally reached and colonized via this process (Nathan et al. 2008, Caughlin and Ferguson 2013).

Effects on germination success

Germination success may be altered via the treatment of a seed in a carnivore's digestive tract and can be differentially affected by various secondary dispersers (Table 1). Improvement in germination success follows if the seeds benefit from a double digestion due to a longer gut retention time (e.g., thick-coated seeds; Nogales et al. 2015) or, possibly, if carnivore feces is richer in nutrients or includes a lower number of competing seeds than that of the primary disperser. Negative effects on germination can result from damage to thincoated seeds due to coarse materials ingested alongside seeds (Traveset et al. 2007). For example, germination success was improved by a secondary dispersal phase by shrikes, but reduced by kestrels (Nogales et al. 2002), and gray herons caused a complete loss of seed viability (Rodríguez et al. 2007, Tables 2 and 3). Variability in carnivore effects on germination success may be related to species-specific gut enzymatic activity and other foods ingested with the seeds (Rodríguez et al. 2007, Traveset et al. 2007). Damage to seeds might also be influenced by the evolutionary past of coexistence of the plant and the secondary dispersal, and the potential for adaptation by the plant to minimize such losses. Plant germination or recruitment is likely also impaired by a deposition in unsuitable microhabitats (e.g., on a road, in poor soil, or in dense vegetation), or at a site that elevates the risk of post-dispersal seed predation. These determinants of dispersal effectiveness are not unique to carnivore-mediated dispersal, but their importance in diploendozoochory remains to be studied.

Interruption of seed predation

Carnivores can also indirectly improve seed viability by interrupting seed predation (Sarasola et al. 2016). Granivorous birds, for example, consume large quantities of seeds that are not immediately destroyed but rather move to the gizzard intact, and are only later broken down and

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Effect of diploendozoochory on plant dispersal success	How is dispersal of	The demonds the second stream to			
	Deposition site	Germination success	the outcome expected to have ecological relevance?		
Seed dispersal success improved	 Longer dispersal distance provides access to newly available habitat suitable for colonization or increases the speed of spread Distance from parent can reduce kin competition, post-dispersal seed preda- tion, and disease mortality Travel between fragments improves plant resilience by maintaining gene flow between populations Better or more varied posi- tions on the landscape are reached because the preda- tor reaches a wider range of suitable sites 	 Seeds benefits from a double digestive process (thick seed coat) Fecal (or regurgitate) nutri- ent content is higher or more suited to the seed's needs than that of primary dis- perser Predation of the primary consumer saves the seed from destruction (seed pre- dation) and thus increases its viability 	 Habitat becomes available for colonization within the secondary disperser's range via fragmentation or changing landscapes The dispersed plant is a pioneer species that requires newly disturbed habitats for establishment The plant is adapted to the alternative habitats made available by the secondary disperser and produces seeds that survive or benefit from two-phase digestion The predator intercepts a significant proportion of seeds transported by an ineffective primary disperser 		
Seed dispersal success lowered	 The predator tends to use habitat that is unsuitable for the plant and that is not used by the primary dis- perser, or deposits seeds in poor locations (e.g., dense vegetation with high compe- tition, or a site with high risk of seed predation or post- germination consumption) Longer dispersal distances take the seed of a specialized or rare plant outside of the species' potential range and thus reduce the plant's effec- tive population size 	 Seed is damaged by double digestion (thin seed coat) or mechanical damage by other, simultaneously inges- ted food items Seeds from multiple prey items may increase the num- ber of seeds in a deposit, leading to increased compe- tition or reduced viability due to release of allelochem- icals from certain seeds that prevent germination of other seeds (Traveset et al. 2007) Nutrient content is lower or less well suited to the seed's needs in the feces or regurgi- tate of the secondary than of the primary disperser 	 Predation on primary dispersers signifi- cantly reduces the proportion of viable seeds entering the seed pool due to reduced germination success or unsuitable deposition sites by the secondary dis- perser A significant propor- tion of seeds of rare or specialized plant species are removed from their suitable habitats by a sec- ondary disperser 		
No significant effect on dispersal success	 The secondary disperser uses similar habitats and does not range significantly wider than the plant's pri- mary dispersers The plant is common and widespread with sufficient population overlap that it does not suffer from reduced gene flow 	 Processing of the seed by the secondary disperser does not change the germination success of the seeds, relative to effects of the primary dis- perser The proportion of a plant's seeds transported by a sec- ondary disperser is very small compared to other means of dispersal 			

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Table I Mechanisms h	wwnich a	nlant'e dienerea	l eniccose le influenced h	wa nredator as	a secondary disperser
Table 1. Micchambino D	y winch a	plain 5 alspeisa	i success is minucrited b	y a predator as	a secondary disperser.

References	Plant species being dispersed	Primary consumer	Type of disperser †	Secondary disperser
Balgooyen and Moe (1973)	Calamagrostis Canadensis	?	NA	American kestrels (Falco sparverius)
Darwin (1859)	Oat, wheat, millet, canary, hemp, clover, beet	Pigeons; speculated: freshwater fish, other prey species	P/NA	Hawks, owls, fishing- eagles, storks, pelicans
Dean and Milton (1988)	Various, most unidentified	Various granivorous birds and mammals	Р	Elanus caeruleus, Falco biarmicus, Tyto alba; inferences for other raptors
Grant et al. (1975)	Chamaesyce amplexicaulis	Finches (Geospiza)	Р	Unidentified owl
Green et al. (2008)	Poaceae sp., Lemna disperma, Myriophyllum crispatum, Nitella sp., Typha dominguensis, Typha orientalis	Unidentified small fish	NA	Australian Pelican (Pelecanus conspicillatus)
Kurek and Holeksa (2015)	Secale cereale, Avena sativa	Speculated: granivorous birds	Р	Foxes (Vulpes vulpes), martens (Martes sp.)
López-Darias and Nogales (2016)	39 (buzzard) and 62 (kestrel) species of mainly weeds, few fleshy-fruited plants	European Rabbits (Oryctolagus cuniculus), Barbary Ground Squirrels (Atlantoxerus getulus), house mice (Mus domesticus), lizards (Gallotia atlantica), unidentified birds	NA	Common Buzzards (<i>Buteo</i> <i>buteo</i>), Eurasian Kestrels (<i>Falco tinnunculus</i>)
Nogales et al. (1996)	Plocama pendula; Rubia fruticose	Lizards (Gallotia galloti)	D	Cats (Felis catus)
Nogales et al. (1998)	Lycium intricatum	Lizards (Gallotia atlantica)	D	Shrikes (Lanius excubitor)
Nogales (1999)	Lycium intricatum	Lizards (Gallotia atlantica)	D	Shrikes (Lanius excubitor)
Nogales et al. (2002)	Lycium intricatum	Lizards (Gallotia atlantica)	D	Shrikes (<i>Lanius excubitor</i>); kestrels (<i>Falco</i> <i>tinnunculus</i>)
Nogales et al. (2007)	Lycium intricatum, Rubia fruticosa, Asparagus nesiotes	Lizards (Gallotia atlantica)	D	Shrikes (Lanius meridionalis); kestrels (Falco tinnunculus)
Nogales et al. (2015)	Plocama pendula, Rubia fruticosa, Juniperus turbinata, Opuntia dilleniid	Lizards (Gallotia atlantica)	D	Cats (Felis catus)
Padilla and Nogales (2009)	Rubia fruticose	Lizards (Gallotia galloti)	D	Eurasian kestrels (Falco tinnunculus)
Padilla et al. (2012)	78 species (26 sp. in shrike pellets, 76 sp. in kestrel pellets)	Lizards (Gallotia spp.)	D	Southern grey shrikes (Lanius meridionalis), Eurasian kestrels (Falco tinnunculus)
Pearson and Ortega (2001)	Centaurea maculosa	Deer mice (<i>Peromyscus maniculatus</i>)	D	Great Homed Owls (Bubo virginianus)
Rodríguez et al. (2007)	at least 12 taxa	Speculated: lizards	D	Grey herons (Ardea cinerea)
Sarasola et al. (2016)	Chenopodium album; Panicum bergii; Sorgum bicolor	Eared doves (Zenaida auriculata)	Р	Cougars (Puma concolor)
Twigg et al. (2009)	speculated: Trifolium sp., Romulea rosea, Poaceae, Hypochaeri ssp., Erodium spp.	European rabbits (Oryctolagus cuniculus)	D	Red foxes (Vulpes vulpes)

† Primary consumer is D = a seed disperser, P = a seed predator, NA = role in seed dispersal uncertain.

digested. Some such seeds survive the digestive process and remain viable (van der Pijl 1982, Orłowski et al. 2016), but consumption of seed predators by carnivores can improve seed dispersal as a larger proportion of seeds are saved from destruction and subsequently deposited by the carnivore. The effect of secondary consumption by the carnivore depends on the number of seeds rescued relative to the number of seeds that would normally enter the seed bank without

Table 3. Evidence of	diploendozoochory	(DZ)	and its	ecological	significance.	For	further	detail	on	the	study
systems, see Table 2	2.										

References	Type of study †, ‡	Evidence of DZ ‡	Ecological significance of DZ §	Relative effect of secondary dispersal ‡, ¶
Balgooyen and Moe (1973)	O; Eg	Viable seeds in R2	LDD; SP-	Not quantified
Darwin (1859)	O; Ef; Eg (F2, R2)	Viable seeds in F2 & R2	LDD; SP-	Not quantified
Dean and Milton (1988)	O; R; Eg (F2, R2)	Viable seeds F2 & R2	ADS; SP-	Not quantified
Grant et al. (1975)	O; E#	Seeds in R2	LDD; SP-	Seeds only found in 2 samples; most seeds tested do not float and have no other mechanism to move between islands
Green et al. (2008)	O; Eg (F2)	Viable seeds in F2	LDD; CFH	4 times more diaspores in pelican feces than in samples collected from other waterbirds (primary dispersers)
Kurek and Holeksa (2015)	O; Eg (F2)	Seeds in R2, some co- occurring with feathers, few seeds viable	SP-	Not quantified, but only 1.1% of samples contained seeds and GR of seeds was very low
López-Darias and Nogales (2016)	O; Eg (R2)	Co-occurring viable seeds and animal remains in R2	LDD	Not quantified; low GR (overall 5%, range: 0-34.7%)
Nogales et al. (1996)	O; R	Co-occurring seeds and animal matter in F2	LDD	Low damage to seeds; 18.9 (<i>Plocama pendula</i>) and 4.8 (<i>Rubia fruticosa</i>) seeds/ lizard dropping, only 0.2 and 0.01 in cats; 66.5% and 80.5% of F1 have seeds, only 7.5 and 3.5% of F2; number of seeds passing through cats is low; possible seed dehydration due to slow F2 breakdown
Nogales et al. (1998)	O, Eg (Pre, F1, R2)	Viable seeds in R2	LDD; ADS; GR+	Higher GR from R2 (64.3%) than from F1 (49.5%) or Pre seeds (54.3%).
Nogales (1999)	O; Eg (Pre, F1, R2)	Co-occurring viable seeds and lizard remains in R2	LDD; ADS; GR+	Higher GR from R2 (64.3%) than from F1 (49.5%) or Pre seeds (54.3%); other effects not quantified
Nogales et al. (2002)	O; Eg (Pre, F1, R2)	Co-occurring viable seeds and lizard remains in R2	LDD; GR-	GR reduced by a third in kestrel R2 relative to F1 and by 25% relative to Pre seeds; GR slightly higher in shrike R2 relative to F1 and similar to Pre seeds.
Nogales et al. (2007)	O; Eg (Pre, F1, R2)	Co-occurring seeds and animal matter in R2	LDD; ADS; GR-	99% seeds undamaged by ingestion, similar GR for Pre and <i>Lanius</i> R2 seeds; 28.2-95.1% reduction in GR in <i>Falco</i> R2, significant differences in microhabitat and dispersal distance relative to primary disperser
Nogales et al. (2015)	Ef; Eg (Pre, F1, F2)	Experimental	GR-; SD-	Seed thickness reduced (sometimes comparably to primary disperser effect), lower GR, disruption of native seed dispersal by an invasive predator
Padilla and Nogales (2009)	O; Ef; Eg (Pre, F1, G1, R2)	Study of kestrel feeding behavior; seeds and lizard remains in R2	LDD; ADS; GR-	G1 discarded by carnivore (89% of seeds) have the same GR as Pre seeds; seeds in F1 have significantly lower GR

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References	Type of study †, ‡	Evidence of DZ ‡	Ecological significance of DZ §	Relative effect of secondary dispersal ‡, ¶
Padilla et al. (2012)	O; Eg (Pre, F1, R2)	Co-occurring viable seeds and lizard remains in R2	LDD; ADS; GR+	Shrikes improve GR of <i>Rubia fruticosa</i> (95% in shrike R2 compared to 80.5% in Pre and 83.0% in lizard F1); no effect on germination of most plant species
Pearson and Ortega (2001)	O; Eg (R2)	Co-occurring seeds and animal matter in feces, one seed viable	IS+	Not quantified but very low GR (<1%) from R2
Rodríguez et al. (2007)	O; Eg (R2)	Co-occurring seeds and animal matter in R2	GR-; IS-	Complete disruption of germination; number of seeds in pellets considered small
Sarasola et al. (2016)	O; Eg (G, F2)	Co-occurring seeds and animal matter in F2	LDD; SP-; IS+	GR similar to seeds in dove gizzards, estimated that cougars could disseminate up to 5000 seeds/ km2/ year
Twigg et al. (2009)	O; Eg (F1, F2)	Viable seeds in F2, some co-occurring with fur	LDD; IS+	Not quantified

[†] Type of study: O = observation, R = review, Ef = feeding experiment, Eg = germination experiment;

¹ The different dispersal stages: "Pre" = diaspores or seeds collected pre-dispersal from the plant or from the ground below the plant; "F1" = seeds recovered from feces of primary disperser; "G1" = seeds recovered from the gizzard or intestine of primary disperser; "F2" seeds recovered from feces of secondary disperser; "R2" = seeds recovered from regurgitate/pellets of secondary disperser.

\$ Ecological significance of diploendozoochory (LDD = Long Distance Dispersal; ADS = Alternative deposition sites; CFH = Continuity in fragmented habitat; SP = Seed predation; SD = Seed dispersal; GR = Germination rate; IS = Spreading of invasive plant species; "-" = reduction in SP, SD, GR or IS; "+" = improvement in SP, SD, GR or IS).

¶ GR = Germination rate.

Flotation experiment.

carnivore involvement (Fig. 1). Dean and Milton (1988) extrapolated that a single raptor might disperse thousands of seeds annually, based on the prey intake rate and the number of seeds in the guts of each prey item. Sarasola et al. (2016) estimated that cougars could disseminate 5000 seeds/km² annually by intercepting seed predation by their main granivorous prey, eared doves. These numbers are only relevant, however, in the context of the total number of seeds produced by plants in the area, and their fates without carnivores (Fig. 1; Appendix S1). These proportions were not estimated in the above two studies and have yet to be assessed in any study of diploendozoochory (see calculations for a potential scenario in the Appendix S1). A step in this direction was taken by Culot et al. (2015), who attempted to quantify the relative importance of secondary dispersal at the microscale by dung beetles, and a similar approach might also prove useful for the study of the phases of diploendozoochory.

Where the carnivore intercepts seed predation, positive effects would, nevertheless, be expected even if overall germination success were slightly lower for carnivore-dispersed seeds than for seeds dispersed by the primary mechanism, given that near-complete seed destruction would be expected from the seed predator. Similarly, positive effects are expected if a carnivore intercepts an ineffective disperser that has a negative or negligible effect on seed germination success, and treatment by the carnivore improves germination success. On the contrary, if a carnivore intercepts dispersal by an effective primary seed disperser, and/or causes a decline in germination success, the dispersal success declines (Fig. 1, Table 1).

Implications of Secondary Seed Dispersal by Carnivores

Human effects: loss of habitat and species

Diploendozoochory may influence plant adaptability to human-altered landscapes and resilience in the face of changing community structures through increased seed dispersal distance, reaching of alternative habitats, or seed germination success. Long-distance dispersal is



Fig. 1. Possible seed fates in systems with diploendozoochory. (A) A plant that relies on animal vectors for dispersal (e.g., fruit-bearing plants) produces a set of seeds. These may remain unconsumed (and therefore less likely to germinate) or be consumed by the primary seed disperser. Seeds deposited by this seed disperser will germinate/ mature at some rate to produce new plants. Some primary seed dispersers will be consumed by the secondary seed disperser (carnivore). Seeds that enter this fate are deposited by the secondary seed disperser and germinate/mature at some rate into new plants. (B) A plant with no obvious adaptations for zoochory produces a set of seeds. Seeds that are not consumed spread via the primary dispersal mechanism (e.g., wind) and germinate/mature at some rate to produce new plants. Some seeds are consumed by a seed predator and destroyed with little chance of germination. Through predation of the seed predator, the secondary disperser diverts some seeds from this fate and instead deposits them. These seeds germinate/mature at some rate into new plants. Illustrations by Kate Broadley.

of increasing importance for ecosystem resilience in the face of environmental changes such as habitat fragmentation and climate change by facilitating rapid dispersal among disconnected areas (Nathan et al. 2008) and by boosting gene flow among populations (Bacles et al. 2006). Escalating habitat loss, fragmentation, and local extinctions due to human actions can disrupt dispersal pathways via declines in the abundance, species richness, and shifting ranges of primary dispersers (Michalski and Peres 2005, Farwig and Berens 2012, Beaune et al. 2013, Caplat et al. 2016) and carnivores that act as secondary dispersers (Crooks and Soulé 1999). The importance of carnivores as dispersal agents might increase in fragmented habitats because they may facilitate plant species' gene flow between fragments due to their larger ranges and often broader habitat use (Carlo and Morales 2016), although the relative importance of the carnivore depends on species-specific responses to fragmentation (Crooks 2002). Some carnivores could even be creating seed corridors between habitat fragments when they defecate more often on linear features such as trails (Suárez-Esteban et al. 2013). Seed dispersal by carnivores thus has the potential to influence the magnitude of detrimental effects of habitat loss and fragmentation on plant communities.

Secondary dispersal by carnivores has the potential to effectively increase the potential speed of plant movements (see Naoe et al. 2016) and colonization of vacant habitat. This may become an increasingly important process at the leading edge of a shifting range due to climate change. The potential involvement of carnivores in seed dispersal processes could shift the predicted outcomes of distribution models (Thuiller 2004) and conservation plans due to their specific role in intercepting seed predation and dispersal, as well as in transporting seeds to novel locations (see also Higgins and Richardson 1999, Caplat et al. 2016, Estrada et al. 2016). As seed dispersal is a key mechanism determining whether plants will be able to shift their ranges to match changing climate conditions (Higgins and Richardson 1999, Chen et al. 2011, Corlett and Westcott 2013), a thorough understanding of dispersal mechanisms is required to predict plant responses to climate change (Cain et al. 2000, Naoe et al. 2016).

The structure of carnivore communities may play a role in determining the utility of secondary seed dispersal. With the exception of the cougar (*Puma concolor*), all documented cases of diploendozoochory to date (Table 2) involved a mesocarnivore. Mesocarnivore release has been well documented where top carnivores have been removed from the landscape by human interventions (Prugh et al. 2009). Globally, a loss in North America (Ripple et al. 2014) and recolonization in Europe (Chapron et al. 2014) of top carnivores might thus have an impact on the efficacy of diploendozoochory, although further research is needed to confirm the role of top carnivores in seed dispersal.

Carnivores could also play a role in stabilizing changes in community structure via their prey selection. A study conducted in the Democratic Republic of Congo found that all seed dispersers in the system were hunted by humans, whereas very few seed predators experienced hunting pressure (Beaune et al. 2013). Such bias in harvest may result in reduced zoochory and thus potentially disrupt ecosystem function by altering plant communities. Likewise, a study in Brazil found frugivores to be the most integral group for ecological network structure, yet also the most threatened by extinction (Vidal et al. 2014). Processes such as these can alter the relative abundance of functional groups (e.g., higher losses of seed dispersers vs. seed predators) and density-dependent prey selection by carnivores could buffer the impact on plant dispersal by targeting the more abundant seed predators over mutualistic seed dispersers. Further research is needed to assess the effects of carnivores on the resilience of plant communities.

The structure and function of ecosystems can be influenced by top-down influences such as trophic cascades (Schmitz et al. 2004), and the involvement of carnivores in shaping the distribution and abundance of plants through diploendozoochory provides additional insights into complex community-level interactions and ecosystem functioning. Carnivores can also have indirect effects on seed dispersal when seed dispersal behavior of the primary disperser (or seed predator) is altered by carnivore presence (Sunyer et al. 2013, Steele et al. 2015).

Invasive plants

Carnivores could facilitate invasions by allowing invasive plants to disperse over a greater distance than they would reach by other means, or by transporting them to a novel location. It has been shown that long-distance dispersal can lead to faster rates of spread (Higgins and Richardson 1996, 1999). A decreased time to germination resulting from a double digestive process may also promote rapid regeneration of invasive plants, which also tend to have adaptations that increase their rate of reproduction (Rejmánek and Richardson 1996, Kolar and Lodge 2001). In at least two cases studied so far, invasive or pioneer plants' viable seeds were indirectly dispersed by carnivores that consumed seed predators (Pearson and Ortega 2001, Sarasola et al. 2016, see also Twigg et al. 2009).

Potential for plant adaptation to diplochory

Dean and Milton (1988) suggested that some plants may be selected to promote, or at least not prevent, seed predation when secondary dispersal by raptors functions as an effective dispersal mechanism. They proposed that this may explain why many seeds consumed by granivorous birds show no obvious adaptations to alternative means of dispersal. For instance, thick seed coats might develop to facilitate long-distance dispersal via a long retention time in a far-ranging animal vector, such as in migrating raptors. This hypothesis might be tested by comparing seed coat thickness or other relevant adaptations on island populations, where thicker coats would be expected on the islands due to increased dispersal requirements from the mainland. Indeed, some evidence suggests that island populations have more thick-coated seeds relative to mainland (van der Pijl 1982, Vargas et al. 2015). Nathan et al. (2008) suggested that not only seed morphology but also fruiting phenology might evolve to match migration schedules of potential dispersers. Plants are most likely to develop adaptations to certain dispersal pathways when the dispersal vectors and dispersion pathways are quite fixed; that is, certain primary and secondary dispersers handle the majority of the plant's seeds. If multiple vectors with different retention times or habitat selection are involved, a range of seed types might be expected to evolve (van der Pijl 1982, Cheptou et al. 2008, Nathan et al. 2008). Disruption of dispersal pathways due to extinctions may have negative implications for such potentially evolved traits (Vander Wall and Longland 2004). If the costs of diplochory (Cheptou et al. 2008, Nathan et al. 2008) are high, owing, for example, to poor seed deposition sites or dispersal out of suitable habitat zone, counter-selection might be expected. Modeling exercises on the potential for plant adaptations to diplochory as well as empirical data on recruitment rates are needed to clarify the adaptive potential of plants to diplochory.

LITERATURE REVIEW

To assess the evidence from empirical research on the significance of diploendozoochory on plant dispersal and broader ecological and conservation implications, we conducted a literature review to identify studies that have observed or empirically tested aspects of diploendozoochory. The search was done in Google Scholar in June 2016 using the search terms diploendozoochory; diplochory; polychory; double endozoochory; secondary seed dispersal; indirect seed dispersal; indirect dispersal; two-phase dispersal; two-stage dispersal; and multi-phase dispersal. From these articles and references therein, we identified sources that empirically addressed secondary seed dispersal by carnivores. For those studies, we identified the plant, primary seed consumer, and carnivore involved. We also recorded any attempts to quantify the relative significance of the second, carnivore-facilitated dispersal stage for the plant's dispersal success. For each study, we collected information on the effects of diploendozoochory on seed viability or germination success, dispersal over long distances or to novel environments, and whether the primary seed consumer was likely to be a mutualistic seed disperser or a seed predator, where these details were reported. We then inferred any likely broader implications of each study from these variables as well as other characteristics of the plants, dispersers, and the ecosystems involved.

Evidence of secondary seed dispersal by carnivores

All but one of the 19 studies that reported diploendozoochory (Table 2) inferred the mechanism from the discovery of seeds in the feces or regurgitates of carnivores that were assumed to not purposely consume seeds (Table 3). The one exception took a purely experimental approach under laboratory conditions (Nogales et al. 2015). The co-occurrence of seeds and remains of potential primary seed consumers in the secondary disperser's excrements (11 studies) was generally accepted as evidence of diploendozoochory (Table 3). The primary consumer of seeds was with certainty a seed predator (granivorous birds) in four studies, and 10 studies involved a primary seed disperser (lizards, a mouse, and a rabbit). The remaining studies were not able to identify the primary disperser with certainty, or it was unclear whether the primary seed consumer was a seed predator or a mutualistic disperser (Table 2).

Studies of diploendozoochory thus far (Table 2) represent a limited range of taxonomic groups. The number of plant species that disperse seeds via diploendozoochory is unknown, as many studies identified only some of the species present among the discovered seeds (range of identified plant species: 0-78 species or 12 taxa; Table 2). Several weeds, grains, and fleshy-fruited plants were among the identified plant species. Of primary seed consumers, only doves, finches, a rabbit, three rodent, and two lizard species have been studied in a natural setting (see also experiments with dead fish by Darwin 1859); in terms of secondary dispersal, two feline, one canine, and one mustelid, as well as several raptors (11 avian species identified, but exact number of species is unknown due to unspecified species in Darwin (1859) and Grant et al. (1975)), have been studied.

Potential significance of diploendozoochory

Overall, there is evidence from the majority of these studies that secondary seed dispersal by predators can have an influence on the components that influence seed dispersal efficiency: Germination success, dispersal distance or the types of habitats reached, and the ecological implications of these studies varied broadly. Carnivores improved seed germination success relative to seeds unprocessed by a secondary disperser in eight studies and reduced germination success in three studies, while two studies observed no change in germination success (Table 3). None of the studies directly tested the germination of seeds consumed by the primary consumer which was subsequently consumed by the carnivore, although an attempt at testing this was made by Nogales et al. (2015). Seven studies compared germination rates between seeds that were not consumed by any animal, seeds that passed through a primary disperser (or were contained in their intestines, Twigg et al. 2009, or gizzards, Sarasola et al. 2016), and seeds that passed through a secondary disperser (Table 3). None of the studies followed germinated seeds through to maturity to assess recruitment rates.

Long-distance dispersal was inferred as the most significant ecological consequence of diploendozoochory in 14 studies, and the secondary disperser used alternative habitats or deposited seeds in novel locations in six studies (Table 3). Secondary dispersal by a carnivore also contributed to the spreading of an invasive or alien plant species in three studies and disrupted their spread in one study. Diploendozoochory resulted in the disruption of seed predation in six studies and the maintenance of connectivity between habitat patches in one study. The disruption of the natural dispersal by an invasive secondary disperser was found in one study (Table 3). Overall, diploendozoochory thus influenced seed dispersal efficacy or potentially the broader plant distribution or communities, but the study designs and the emerging patterns are currently too diverse to permit definitive conclusions about the exact significance of the phenomenon across systems.

FUTURE DIRECTIONS

While the circumstantial evidence and the projected potential frequency of secondary dispersal events suggest that diploendozoochory is not uncommon, systematic research into diploendozoochory is needed to better understand the phenomenon and its overall ecological significance. While carnivores may have a significant influence on seed dispersal patterns under the conditions we have described in Table 1, evidence should be carefully weighed before assuming diploendozoochory is relevant ecologically or otherwise (e.g., suggested ecosystem services, Sarasola et al. 2016, see also Appendix S1). Continuing developments in methodology, such as the use of DNA barcoding, molecular "log books," stable isotopes, and radio-active tags along with a mechanistic vectorcentered approach to study seed dispersal (Bullock et al. 2006, Nathan et al. 2008, Fordham et al. 2014, González-varo et al. 2014, Culot et al. 2015, Herrmann et al. 2016, Naoe et al. 2016), make aspects of the phenomenon more readily testable. Future studies should explicitly address the potential mechanisms and implications of the phenomenon among systems. In the face of the changing landscapes, it would be especially important to look for further evidence of the influence of diploendozoochory on metapopulation dynamics in fragmented environments, on the role of carnivores in disrupting or facilitating the spread of rare or invasive species and recolonizing degraded habitats.

To rigorously assess the significance of diplochory, the relative proportions of seeds with various fates must be determined (Culot et al. 2015, Fig. 1; Appendix S1). For a controlled experimental approach, known quantities of seeds from known plants would need to be fed to primary consumers (dispersers and seed predators), and a proportion of these consumers then exposed to predation by secondary dispersers. The droppings and pellets of each disperser, as well as the intact, unconsumed seeds, would then be collected and the viability of seeds therein assessed via germination experiments (preferably on actual site of deposition). Furthermore, recruitment of the seedlings should be monitored because the survival of the seedlings to maturity and their subsequent reproduction are relevant for assessing the evolutionary significance of the different dispersal syndromes (Schupp and Jordano 2010).

Effects of diploendozoochory on seed fates can be most readily quantified when a single animal species is responsible for the majority of primary dispersal or seed removal of a given plant species, and a single carnivore is responsible for the majority of the mortality of the primary vector. In such systems, the effect of the carnivore is also likely the highest, and plant adaptations to diploendozoochory might therefore be expected to evolve. Relatively simple systems with limited species interactions would thus likely prove most fruitful for the study of the phenomenon (such as the raptors, lizards, and *Lycium* fruit studied in an island ecosystem; Nogales 1999) as seed fates of complete seed cohorts could potentially be followed throughout the dispersal pathway. Invertebrate primary dispersers with reasonably small-ranged carnivores, such as insectivorous reptiles, might also prove useful because of their relatively short dispersal distances. However, multiple taxa should eventually be studied to determine how widespread the phenomenon really is and its potential management and conservation consequences (Levey et al. 2002).

Although recent studies of two-phase dispersal have focused on raptors and mammalian carnivores as well as their prey (typically small mammals, birds, and reptiles), numerous other taxa disperse seeds and eat seed dispersers or seed predators, suggesting multiple pathways of twophase dispersal have yet to be identified. For example, crocodilians are thought to serve as potential secondary (as well as primary) dispersers of up to 46 plant genera, although the effects on seed viability is unknown and the existence and frequency of diplochory remains to be confirmed (Platt et al. 2013). Diploendozoochory may also occur in systems where invertebrates and fish function as primary dispersers (Darwin 1859, van der Pijl 1982, Pollux 2011). These animals are often eaten whole and consumed in large quantities by birds and mammals, sometimes followed by long-distance movements by the secondary disperser (Green and Figuerola 2005). Some taxa, such as omnivorous primates, may include species that serve as both a primary and a secondary disperser by consuming small prey items, such as insects along with fruit (e.g., mouse lemurs; Dammhahn and Kappeler 2008) and falling prey to raptors, snakes, and mammalian carnivores (Rasoloarison et al. 1995).

Conclusions

Several authors have suggested that polychory is likely a much more common phenomenon than has been previously assumed (Ozinga et al. 2004, Vander Wall and Longland 2004) and can be more beneficial for the dispersing plant than single-phase dispersal (Vander Wall and Longland 2004). While these studies have largely concentrated on abiotic vectors and short-distance, second-phase dispersal by invertebrates and scatter-hoarding rodents, the impact of carnivores may be similarly important, particularly in discontinuous habitats. Secondary dispersal by carnivores is by no means exclusive of the types of diplochory defined by Vander Wall and Longland (2004); rather, it is very likely that further seed transport by ants, dung beetles, or scatterhoarding rodents often occurs after seeds are deposited by the secondary disperser.

Our framework provides guidelines for future research, with predictions that should aid in targeting systems that are likely to be most affected by carnivore involvement in seed dispersal. In addition to disrupting heavy seed predation pressure, carnivores that intercept large proportions of a plant population's seeds and significantly alter the germination or recruitment success of seeds relative to the primary disperser will most likely be an important ecological force for the plant species and, possibly, the community structure.

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Another important role for far-ranging secondary dispersers may involve long-distance dispersal or gene flow between remote populations or habitat fragments. While carnivore effects will likely be small in most systems, such circumstances may indeed result in secondary seed dispersers significantly influencing plant range shifts, dispersal success, fitness, and potentially species viability.

It is currently unknown how important the phenomenon is ecologically, but given its potentially vast prevalence and the possible implications, it is possible that ignoring it could impair the interpretation of broad ecological patterns or hinder conservation efforts. Considering diploendozoochory as a part of the dispersal mechanism of plants can potentially improve modeling outcomes for range shifts due to climate change, or help explain current plant distributions, as historical effects of carnivores (or other large-bodied animals; Pakeman 2001) may have influenced plant movement rates. Where the secondary disperser facilitates different dispersal processes than are accomplished by other means of dispersal, carnivore involvement may have important consequences for the spread of invasive plant species, as well as the ability of plants to adapt to habitat loss and changing climatic conditions. Where such relationships exist, the extinction or decline of involved species can affect multiple trophic levels and disrupt ecosystem functions.

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