

## Forum

### A seed dispersal effectiveness framework across the mutualism–antagonism continuum

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Many angiosperms rely on vertebrates for seed dispersal via gut passage, an interaction that has been traditionally classified as a mutualism. The seed dispersal effectiveness (SDE) framework provides a mechanistic approach to evaluate evolutionary and ecological characteristics of animal-mediated seed dispersal, by synthesising the quantity and the quality of the dispersal that a plant species receives from each of its animal dispersers. However, the application of the SDE framework has been largely restricted to plant–frugivore interactions, whereas animal-mediated seed dispersal results from plant–disperser interactions that cover a continuum from pure mutualisms to antagonisms. This biases ecological and evolutionary knowledge on plant–disperser interactions. Here, we propose an extended SDE framework (‘eSDE’) that allows comparing plant–disperser interactions in the full mutualism–antagonism continuum ranging from pure mutualisms (frugivores) to conditional mutualisms (scatter-hoarding granivores and folivores) and antagonisms (pure granivores). We present the eSDE framework, and use examples to illustrate how it can be applied to compare effectiveness among plant–disperser interaction types. Our initial comparison based on available data suggests that vertebrate species differ more in the number of seeds they deposit away from the mother plant (quantity), than in the effects such dispersal processes have on seed fate (quality). Scatter-hoarding granivores provide the most effective dispersal due to high removal rates, closely followed by frugivores due to high deposition rates. Folivores and pure granivores provide low quantity dispersal, but of high and moderate quality, respectively. These early comparative insights illustrate the necessity and usefulness of more standardized data collection protocols, for which we provide recommendations. Applying the eSDE framework can reveal broad-scale patterns across and within plant–disperser interaction types, which will advance our evolutionary understanding of plant–animal interactions. This will provide new insights into the consequence of anthropogenic impacts on vertebrate-mediated seed dispersal in a world in which plant–animal interactions are increasingly threatened.

## Introduction

The dispersal of fleshy-fruited plant species by frugivores is an important ecological mutualism (Jordano 2000, Bronstein 2001, Carlo et al. 2022) that is involved in processes of (diffuse) coevolution (Herrera 1984). Frugivores can disperse seeds through defecation following ingestion of the whole fruit (endozoochory) or by spitting and accidentally dropping of seeds while consuming the fruit's pulp. Vertebrate plant consumers such as herbivores and granivores also disperse a broad range of plant seeds, however, many of these seeds lack attractive nutritious pulp (Howe and Smallwood 1982, Soons et al. 2016, Gómez et al. 2019, 2022, Green et al. 2021). While in lowland forests and woodlands species from tropical forests showing fruits with pulp may predominate, in other bioclimatic regions fleshy fruits may be relatively rare (Yu et al. 2017, 2021, Wang et al. 2022). Seed dispersal by herbivores and granivores is traditionally considered an antagonistic interaction modulated by a different suite of (co)evolutionary processes than frugivory – such as defence–offence and compensatory strategies (Augustine and McNaughton 1998, Karban and Agrawal 2002, Benkman 2010, Cao et al. 2022).

The distinction between mutualistic and antagonistic interactions stems mainly from the key role attributed to the presence of fruit flesh, which has putatively evolved especially to reward and attract particular endozoochorous seed dispersers (McKey 1975, Wheelwright and Orians 1982). However, making this distinction disregards the importance of other

plant parts that may be rewards to consumers. For instance, small seeds may be ingested and dispersed by herbivorous animals that feed mainly on nutritious plant foliage (leaves and shoots; 'folivores' hereafter), known as the 'foliage-is-the-fruit' hypothesis (Janzen 1984). The foliage might then provide these animals with attractive resources analogously to how fleshy pulp can stimulate ingestion of seeds by frugivores (Janzen 1984). Likewise, large or abundant seeds can be seen as rewards to dispersers (Jansen and Forget 2001, Perea et al. 2011, Arnan et al. 2012). If we also consider alternative rewards than fruit pulp to plant consumers, such as the energy contained in plant foliage or the portion of digested seeds, the binary classification of mutualism versus antagonism no longer holds, but rather becomes a continuum. From an evolutionary perspective the relative importance of the antagonistic versus mutualistic components of a plant–disperser interaction becomes primarily determined by the outcome of the interaction: if the interaction benefits seed dispersal it may be considered a mutualism (Bronstein 1994, Connor 1995, Gómez et al. 2019). Hence, if there are costs imposed by the seed ingestion, the interaction also has an antagonistic component – whether this is the consumption of foliage, other seeds or even nutritious pulp. Interactions with animals that have primarily diets as frugivores, folivores, scatter-hoarding granivores (presenting hoarding behaviour, hereafter scatter-hoarders) or non-hoarding granivores (those without hoarding behaviour, hereafter granivores) have outcomes that can be placed along a mutualism–antagonism continuum, as proposed in Fig. 1.

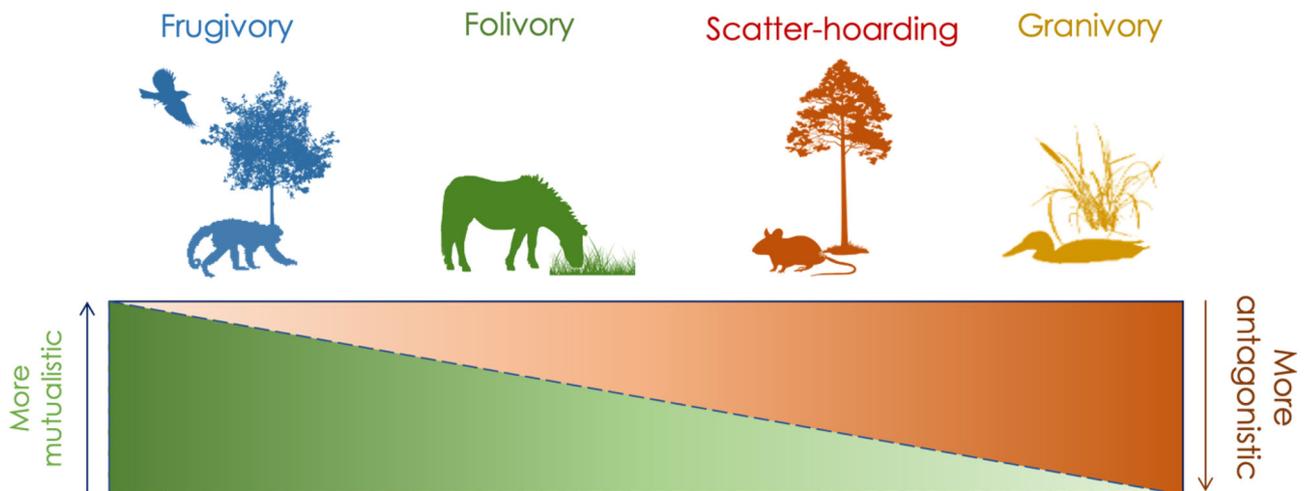


Figure 1. Illustration of the mutualism–antagonism continuum, with expected differences among animal groups based on their dominant diet components: frugivores, folivores, scatter-hoarders or granivores. Based on the fraction of seeds surviving digestion and on the expected treatment in the consumer's gut, we expect a gradient of decreasing dispersal effectiveness from left to right. It is important to note here that this dietary categorization, broadly used in animal ecology and evolution, includes considerable variability and should be taken to refer to the main component of the animal's diet – which generally involve clear adaptations of the digestive anatomy, physiology and behaviour. To account for such variability, we have included information on the diet composition of all animal species in our dataset in the Supporting information and encourage researchers targeting these kinds of comparisons in the future to provide similar information.

As long as some seeds survive, any plant–animal interaction resulting in dispersal can contribute to plant fitness. Predictions of fitness benefits of these interactions to plants do not only depend on seed survival, but can be developed more inclusively using the seed dispersal effectiveness (SDE) framework as initially proposed by Schupp (1993) and reviewed by Schupp et al. (2010, 2017). The SDE framework expresses the fitness benefits of plant–disperser interactions to the plant (named ‘seed dispersal effectiveness’) as the product of a quantity and a quality component. SDE is the product of the number of ingested seeds (i.e. seed dispersal quantity), and the fate of dispersed seeds extended from all events taking place from their ingestion in a given site until reaching the adult plant stage (i.e. seed dispersal quality).

Over the last three decades, the SDE framework has become a standard method for comparing the benefits to plants among plant–disperser interactions – and has been widely applied to plant–frugivore systems (Jordano and Schupp 2000, Rother et al. 2016, Culot et al. 2017) and, less frequently, to plants dispersed by scatter-hoarding birds and rodents (Hollander and Vander Wall 2004, Gómez et al. 2008). While the original framework initially targeted comparisons in effectiveness among frugivorous dispersal systems, later work extended the application to other types of mutualistic interactions, such as plant–pollinator and plant–mycorrhiza interactions (Schupp et al. 2010, 2017). However, the original SDE framework was specifically suitable to study plant–frugivore interactions, with methods and metrics clearly streamlined to study the outcome of frugivory; and its extension to include folivores, scatter-hoarders or granivores has proven challenging.

Here, we propose an extension of the SDE framework that covers the full range of plant–disperser interactions in the mutualism–antagonism continuum; from what we classically consider pure mutualisms (frugivory) to pure antagonisms (granivory), including conditional mutualisms (scatter-hoarding and herbivory). First, we introduce an extended SDE framework (hereafter ‘eSDE framework’) that includes plant–disperser interactions across the whole mutualism–antagonism continuum, in which we explicitly define the quantity and quality components as multiplicative probabilities associated with specific plant demographic processes. This allows the calculation of SDE and all its components as fitness per produced seed. Second, we provide recommendations on how current dispersal methodology can be standardized across plant–disperser interactions, to facilitate direct comparisons across the full range of plant–disperser interactions. Third, we illustrate how one can apply the extended framework to compare eSDE metrics among frugivores, folivores, scatter-hoarders and granivores, based on an illustrative dataset of 53 plant–disperser interactions that could be assembled from the literature. We expected seed dispersal effectiveness to decline along the mutualism-to-antagonism gradient (i.e. in the order mentioned here and as depicted in Fig. 1). Last, we propose future applications of the eSDE framework.

## A framework for the mutualism–antagonism continuum

The SDE framework was originally introduced to provide ‘a quantitative framework for estimating the contributions of individual dispersal agents to plant fitness’, with seed dispersal effectiveness representing ‘the contribution a disperser makes to the future reproduction of a plant’ (Schupp 1993, Schupp et al. 2010). The original framework considered effectiveness as ‘the number of new adult plants produced by the dispersal activities of a disperser’. Its calculation involves a quantitative and a qualitative component.

Dispersal quantity is the product of the number of visits made to the plant by a disperser and the number of seeds ingested per visit. In demographic terms, this component represents the transition probabilities associated with a dispersal phase, from ‘sired seed’ to ‘deposited seed’ – with two sub-components: seed removal probability and seed deposition probability. Dispersal quality is the product of ‘seed treatment’ (the effect of passage through the disperser on seed viability and germination) and ‘seed deposition’ (the probability that a deposited seed will survive and establish at a given deposition site). In demographic terms, the qualitative component represents the transition probability associated with an establishment phase, from a ‘deposited seed’ to an ‘adult plant’ – consisting of three probabilities: the probability of surviving post-deposition seed predation, the probability of germination (as affected by handling and/or gut passage) and the probability of establishment of seeds as young plants (or ideally, to adult plants). The quantity and quality components multiply to yield offspring fitness (adult plants per sired seed), which can be plotted in a two-dimensional representation of the ‘SDE landscape’, with SDE isoclines representing lines of equal fitness for the next generation (Schupp et al. 2010).

### Extending the methodology – quantity

In the original SDE framework, quantity was defined as the product of the number of visits of an animal to a fruiting plant and the number of seeds ingested per visit (Schupp et al. 2017). The probability that a dispersed seed survives handling by the dispersal agent is considered in the quality component. This is probably a consequence of the framework being pioneered and inspired by avian frugivorous systems where most, or at least a large fraction of, ingested seeds may be excreted viably. However, for the majority of other systems, considering that seeds that are digested are a sensible proxy for the proportion of seeds actually dispersed is not appropriate (Simmons et al. 2018). We therefore suggest that focusing on the number of seeds that are physically displaced by an animal, rather than on the number ingested as its quantitative contribution to the dispersal process, will provide the most ecological informative metric.

This proposed division provides a clear, objective landmark for the quantification of the two phases of the dispersal processes: a pre-deposition phase (from removal to deposition

as quantity) and a post-deposition phase (where seed fate is influenced by the indirect impact of the dispersal processes on deposition, i.e. post-deposition as quality). The pre-deposition phase (quantity) includes all spatial processes involving a direct interaction between the plant and the disperser. Seed destruction during mastication or gut passage is a component of this interaction, which only takes place while the seed is being manipulated or digested by the animal vector. After deposition, the interaction between the plant and animal ceases completely. The post-deposition phase (quality) then starts at the deposition site. Because the spatial dispersal process represents the movement of each seed from the mother plant to a deposition site, it feels erroneous to consider seeds that are predated on the mother plant (i.e. those that are masticated or digested in the gut by the animal vector) as actually dispersed. In our view, ‘dispersal quantity’ is ecologically best defined as the number of seeds completing the journey from the mother plant to any given deposition site.

We propose an eSDE framework (visualized in Fig. 2) with three modifications to the quantity component. First, we define quantity as ‘the proportion of viable seeds produced by a mother plant deposited away from the place where they were encountered’. This means that the destruction of seeds before deposition, caused by their manipulation, ingestion and gut passage, becomes included in the quantity component (instead of originally the quality component). Second, to obtain comparable estimates that represent the fitness contribution of dispersal quantity, this estimate must be reliably sampled along the complete fruiting period. This can be done during the entire period or only at representative regular intervals, after which the obtained estimates can be multiplied by the duration of the entire fruiting period

to obtain the total number of seeds dispersed per plant per season (for practical reasons, we are obviating the necessity of multiplying these by the lifespan of the mother plant). Third, many herbivorous and granivorous animals forage on meadows where the number of individual adult plants cannot be estimated (e.g. the vast majority of estimates for herbaceous plants are given in relative frequencies or proportions). In addition, many animal vectors ingest fruits or seeds after they have been displaced away from the mother plant by wind or water – e.g. in diplochory by waterbirds. Other frugivores consume the fleshy pulp and spit the seeds (e.g. Samango monkeys spitting toxic seeds of *Clivia miniata* (Kiepiel and Johnson 2019); peccaries and other ungulates spitting the seeds of some palm species (Keuroghlian and Eaton 2008, Delibes et al. 2019)). Another mechanism of seed dispersal takes place when granivores accidentally lose seeds during transport, known as dyszoochory (Vittoz and Engler 2007). Hence, for many zoochorous dispersal systems, alternative methods than direct measures of ingestion from plants are necessary to estimate dispersal quantity – such as the combination of foraging rates (seeds consumed/unit time/unit area), foraging periods (units time/foraging season) and seed crop (seeds/unit area), e.g. in grasslands, aquatic meadows and seedbanks deposited on the ground; or the combination of total fruit consumption (consumption by all frugivores for the whole fruiting season) and relative fruit consumption by each different frugivore – estimated during specific intervals interspersed over the entire fruiting season.

Consequently, to accommodate these different approaches in a conceptually consistent definition that adequately refers to offspring fitness, we calculate the proportion of produced seeds that have been effectively dispersed, i.e. effectiveness

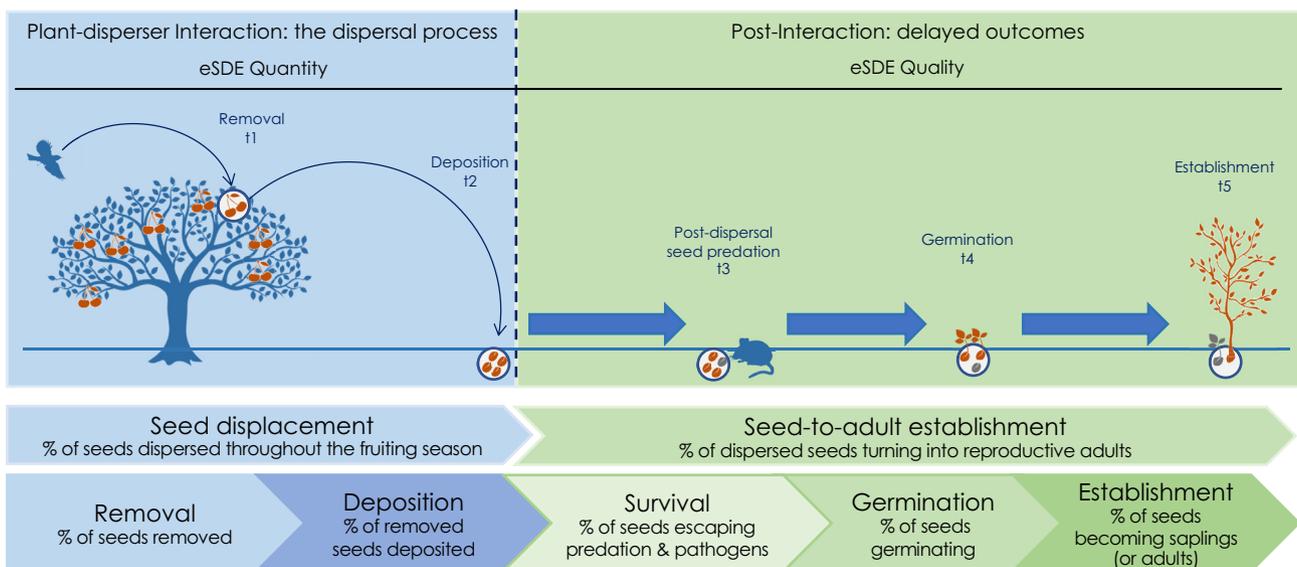


Figure 2. Visualization of the extended seed dispersal effectiveness (eSDE) framework, with its quantity and quality components shown in different colours. The quantity component (left, in blue) consists of seed removal ( $t_1$ ) and deposition ( $t_2$ ). After this process of seed displacement, three post-interaction processes determine the quality component (right, in green): seed predation ( $t_3$ ), seed germination ( $t_4$ ) and seedling establishment ( $t_5$ ). Grey symbols indicate the proportion of seeds or seedlings that is lost during each of the steps. In this example, deposition of four seeds from the mother plant results in one established young plant. Based on Schupp et al. (2017).

on a per seed basis. Besides the practical advantages outlined above, such a definition provides a more rigorous assignment of fitness effects (avoiding the numerous assumptions involved in assigning offspring fitness to parental fitness (Wolf and Wade 2001)) and eliminates the interference of mother plant fecundity on eSDE estimates (thus allowing for the analysis of the effect of maternal traits such as fruit crop and/or fruiting phenology on eSDE).

### Extending the methodology – quality

In the original framework, quality is considered the probability that a dispersed seed establishes a reproducing adult plant. This is calculated as a combination of the probability of an ingested seed to remain viable after gut passage, germinate to produce a seedling and subsequently survive until adulthood. We propose two extensions.

First, the component of gut passage survival becomes included in the quantity component of eSDE. Second, we explicitly include the effect of differential deposition in different microhabitats in the calculation of all quality sub-components. This provides the option to incorporate landscape heterogeneity into estimates of effectiveness. We propose to do this by 1) quantifying the proportion of seeds deposited per microhabitat (or patch); 2) providing separate estimates per microhabitat for the survival to post-dispersal seed predation, the rate of seed germination and seedling-to-young-plant survival; 3) multiplying these sub-components to estimate the quality component per microhabitat; 4) adding these components, weighted using the proportion of deposition at each microhabitat, to calculate the overall quality. This possible extension facilitates incorporating the heterogeneity of the landscape into eSDE calculations and including estimates of the effects of dispersal distance on eSDE. Examples are provided in the Supporting information. In the simplest case, distance can be directly incorporated by treating different distance categories as microhabitats for differential deposition. Including differential deposition is no prerequisite for the eSDE framework to function.

We define the quality component per seed – as ‘the proportion of dispersed seeds turning into reproductive adults’ (or, in most available frugivore studies, into young plants). This makes quality the probability that a deposited seed escapes post-dispersal seed predation, germinates and becomes an adult (or young plant). This multiplicative probability can be multiplied by the dispersal quantity component (also on per seed basis) to provide an estimate of the offspring fitness, as follows:  $eSDE = eSDE_{ql} \times eSDE_{qt} = (\text{seeds deposited/seed sired}) \times (\text{reproductive adults/seed deposited}) = \text{reproductive adults/seed sired}$  (Fig. 2).

### Approaches to determine eSDE quantity

Obtaining reliable estimates of dispersal quantity, particularly those involving the identification of dispersal events in the field, is often challenging but of utmost importance to obtain robust estimates of eSDE. To guide the future advancement

of this task, we complement the guidelines on how such estimate could be made in Table 1a with suitable examples that may be found in the references listed in the Supporting information. We distinguish four approaches to estimate the quantity component of the eSDE framework (Table 1a), which apply to frugivory and scatter-hoarding (approach 1 and 2) and folivory and granivory (approach 3 and 4). In the former two, it is possible to observe the animal disperser’s visit to individual plants and quantify fruit consumption, in the latter two it is not.

In approach 1, observers quantify the disperser’s visitation rate (number of visits per unit time) and fruit removal rate (number of fruits removed per unit time) per individual mother plant; and combine these two metrics to obtain the number of fruits (or seeds) removed per unit time (Herrera and Jordano 1981, Rother et al. 2016). Fruit removal per unit time should be extrapolated to fruit removal over the complete fruiting season, by multiplying with an estimate of the duration of the fruiting season. This estimate should then be divided by the fruit crop (number of fruits per plant). Seed removal probability may then be combined with the seed deposition rate (number of seeds deposited per seed removed), which can be estimated using field observations (measuring e.g. the proportion of dropped, regurgitated and/or defecated seeds) and/or experiments in captivity (measuring e.g. gut passage rate of ingested seeds), to calculate the quantity component (seeds deposited per seed produced by the mother plant, Coates-Estrada and Estrada (1988)).

Frugivory studies often use a simpler approach to calculate fruit (or seed) removal over the full fruiting season (approach 2, Martínez et al. 2008, Culot et al. 2017, McConkey et al. 2018). This involves the combination of two metrics: total fruit removal, estimated e.g. by periodically counting fruits in marked branches, and measuring the proportion of unconsumed, fallen fruits (e.g. using collectors placed under the mother plant), until the end of the fruiting season; and estimating the proportion of removal exerted by each different animal vector, using direct or indirect (e.g. camera-traps, DNA-barcoding) observations (Quintero et al. 2022). Alternatively, total consumption can be estimated by comparing (standing and fallen) fruit crops in excluded and open (control) plants (Rodríguez-Pérez and Traveset 2010). Seed removal probability (seeds removed per seed produced by the mother plant) per vector species can be estimated directly by multiplying the two aforementioned variables: the proportion of seeds removed from the mother plant (fruits removed/fruits available) times the proportion of seeds removed by each different vector (fruits removed by vector *i*/fruits removed by all vectors, for the total observation time sampled). Seed removal estimates can then be combined with seed deposition rates (estimated by analyses of faecal samples or via feeding experiments, as described for approach 1) to obtain the eSDE quantity component.

Scatter-hoarding studies use slight modifications of approach 2 (Table 1a), by combining estimates of total fruit crop fallen under mother plants with estimates of seed removal. The latter may be derived from field surveys

Table 1. Overview of possible approaches for calculating the quantity and quality components of seed dispersal effectiveness for the eSDE framework. (a) Four different approaches and their associated metrics for calculating eSDE quantity. (b) One approach to calculate eSDE quality that can be adopted across all vector types. For each of these approaches, we indicate 1) the formulas that can be used to calculate dimensionless probabilities; 2) the parameters in the formulas; 3) the units of the parameters; 4) the type of data collection required; and 5) the vector type to which the approach can be applied. For data examples we refer to the Supporting information.

	Formulas and parameters	Parameter units	Data <sup>1</sup>	Vectors <sup>2</sup>
<b>(a) eSDE quantity</b>				
Approach 1. Observations of visitation and fruit-consumption rates <sup>3</sup>	$(VR \times FR \times LFP/FC) \times SDR$			Fr,SH,(G,E)
	VR: visit rate	no. of visits day <sup>-1</sup> plant <sup>-1</sup>	FO	
	FR: fruit removal	no. of fruits visit <sup>-1</sup>	FO	
	LFP: length of fruiting period	no. days	FO	
	FC: fruit crop	no. of fruits plant <sup>-1</sup>	FO	
	SDR: seed deposition rate	dimensionless (no. of seeds deposited no. seeds removed <sup>-1</sup> )	FO, EO	
Approach 2. Observations of cumulative consumption in marked plants/branches <sup>3</sup>	$\%TC \times \%FR \times SDR$			Fr,SH,(G,E)
	%TC: fruits removed by all frugivores/fruit crop (or subsample of fruits marked)	dimensionless (no. of fruits/ no. of fruits)	FO	
	%FR: fruits removed by focal frugivore/fruits removed by all frugivores	dimensionless (no. of fruits/ no. of fruits)	FO, F+L, FE	
	SDR: seed deposition rate	dimensionless (no. of seeds deposited/no. of seeds removed)	FO, F+L, EO	
Approach 3. Backwards estimate from seeds found in droppings	$SD \times DR \times FP \times DAB/SC$			(Fr),Fo,G
	SD: seeds per dropping	no. of seeds dropping <sup>-1</sup>	F+L	
	DR: defecation rate of disperser	no. of droppings individual <sup>-1</sup> day <sup>-1</sup>	FO, EO	
	FP: foraging period	days	FO	
	DAB: disperser abundance	no. of individuals m <sup>-2</sup>	FO	
	SC: seed crop	no. of seeds m <sup>-2</sup>	FO, F+L	
Approach 4. Inverse estimate from seeds found in droppings	$\%SD \times TSD/SC$			Fo,G
	TSD: total seed deposition (in dung) per unit area	no. of seeds m <sup>-2</sup>	FO, F+L	
	%SD: seeds of focal plant species/seeds of all species (both deposited in dung)	dimensionless (no. of seeds/ no. of seeds)	FO, F+L	
	SC: seed crop per unit area	no. of seeds m <sup>-2</sup>	FO, F+L	
<b>(b) eSDE quality</b>				
Approach. Measuring the fate of seeds, seedlings or young plants	$\Sigma SDi \times (SPPi \times SGPi \times SYSi \times YASi)$ where i = different microhabitats			All vectors
	SD: seed deposition per microhabitat (seeds deposited at focal microhabitat/seeds deposited at all microhabitats)	dimensionless	FO	
	SPP: survival to post-dispersal seed predation: no. of seeds surviving no. of seeds deposited <sup>-1</sup> = 1 - (no. of seeds predated no. of seeds deposited <sup>-1</sup> )	dimensionless	FO, FE	
	SGPi: seed germination: no. of seedlings no. of seeds <sup>-1</sup>	dimensionless	FO, FE	
	SYSi: seedling to young plant survival: no. of young plants no. of seedlings <sup>-1</sup>	dimensionless	FO, FE	
	YASi: young plant to adult survival: no. of adults no. of young plants <sup>-1</sup>	dimensionless	FO, FE	

<sup>1</sup> Data indicates the type of data collection required: FO: field observations and measurements (e.g. direct observations, camera traps, fruit removal in marked branches). F+L: field collection + lab analysis (or greenhouse germination). FE: field experiments (fruit offers with camera traps, seed predation experiments, in situ germination tests). EO: experimental observations (e.g. captive animals, laboratory).

<sup>2</sup> Vector indicates for which disperser an approach is suitable: Fr: frugivores. G: granivores. Fo: folivores. SH: scatter-hoarders. Letters in brackets indicate suitable methods for which no example was reviewed in our dataset. Approaches suitable for epizoochory studies are also indicated with an E.

<sup>3</sup> Note that for approach 1 and 2 the calculation method used eliminates the need to estimate seeds per fruit.

(e.g. monitoring of fruits using camera traps, Hirsch et al. 2012a, Midgley et al. 2017) or by measuring seed removal from experimental exclosures or enclosures (Hollander and Vander Wall 2004, Gómez et al. 2008). An additional complexity of these systems arises from the habit of scatter-hoarders to revisit seed caches and either consume the seeds or move them further (Jansen et al. 2012). Careful experiments with marked or labelled seeds have been used to estimate the ultimate position and fate of cached seeds, allowing for an estimate of both seed deposition rates (seeds deposited at the end of the dispersal season) and differential seed deposition at different microhabitats (a key variable to estimate SDE quality, see below) (Hirsch et al. 2012b, Kuprewicz 2013). Caches can also be robbed by different dispersers, a process amenable to secondary seed predation that adds to the reduction in seed deposition caused by revisits by the cache owner – thus making these two components of eSDE difficult to distinguish in scatter-hoarding systems (Jansen et al. 2012).

For folivores and granivores, seed consumption is often difficult to infer from direct observations, since consumption is often hidden – e.g. small seeds consumed while embedded in foliage, or seeds extracted by consumers from aquatic seed banks through filtering of the sediment. One approach is to use methods amenable to approach 1, by combining estimates of total plant consumption (number of bites per unit time multiplied by foliage mass consumed per bite, as in Cosyns et al. (2001)) with estimates of seed crop (number of seeds per unit foliage mass), and scaling these over time and space. Another approach is to compare seed removal inside and outside exclosures, which has been used to quantify seed ingestion by waterbirds (Callicutt et al. 2011, Hagy and Kaminski 2012). However, the most common approach is to combine estimates of the number of viable seeds deposited in droppings (number of seeds per unit dropping mass) with estimates of the disperser's defecation rate (dropping mass per unit time) and the duration of the foraging period (during which seeds are available for consumption) (Cosyns et al. 2005a, Lamoot et al. 2005, Martín-Vélez et al. 2021). The combination of these three estimates (approach 3 in Table 1a) provides seed deposition per individual disperser (accumulated for the whole fruiting season), which may be expressed as eSDE quantity (seeds deposited per seed available at the meadow or seed bank) by multiplying by the density of dispersers (number of individuals per unit area) and dividing by the fruit crop (number of seeds available per unit area).

Approach 4 uses a simplification analogous to approach 2 (Table 1a). It estimates total seed deposition in dung, per unit area and over the entire fruiting season (using adequate sampling schemes), by multiplying seedling emergence from samples of dung by total dung deposition per unit area (Cosyns et al. 2005a). Dividing this estimate by the seed crop (as number of seeds per unit area) provides eSDE quantity (number of seeds deposited per seed produced by the plants, both in a given area). The seed removal component can be calculated by dividing by the seed deposition rate (gut-passage rate), as in approach 3.

## Approaches to determine eSDE quality

The quality component of eSDE is generally estimated from field observations and trials (Table 1b). It can be estimated as the multiplication of three sub-components, which always involve the calculation of survival or transition rates from the monitoring (repeated observations) of marked seeds (growing from seeds to seedlings to young plants, see Jansen et al. (2004) for an example).

Dispersed seeds may be deposited in different microhabitats, whose impact on the subsequent seed fate is often a major determinant of eSDE. Hence, to estimate dispersal quality, both the proportion of seeds deposited at each microhabitat type and the impact of microhabitat type on the different quality sub-components (post-dispersal seed predation, seed germination and seedling establishment to the young or adult plant stages) must be quantified. Examples of relevant different deposition microhabitats include open areas with bare soil; areas covered by specific plant species or vegetation types; specific types of refugia (e.g. rock crevices); specific patches, e.g. wetlands within a terrestrial matrix; and/or specific ranges of distances to the mother plant. Microhabitat categorization can be included in the eSDE framework and is likely to be of considerable importance for SDE estimates, but its inclusion is no prerequisite for use of the framework.

Post-dispersal seed predation, the first sub-component of quality, is usually estimated by means of field observations (e.g. regular observations of marked seeds or seed caches, as in McConkey et al. (2018)), tagging (e.g. tracking of seeds with tags (Forget 1990, Hollander and Vander Wall 2004, Gómez et al. 2008, Hirsch et al. 2012a)) and/or field trials (e.g. monitoring the fate of seeds offered to dispersers/predators, e.g. on the floor, at simulated caches or within dung piles (Garcia et al. 2005, Kuprewicz 2015, Culot et al. 2017, Neghme et al. 2017)), sometimes aided by camera-traps to differentiate secondary dispersal from post-dispersal predation (Hirsch et al. 2013). The survival probabilities are directly amenable for eSDE calculations. One of the most common caveats of some of these observations concerns the period of time measured: ideally, the measurement should include the complete period from deposition to germination (or viability loss) or be adequately designed to allow for such an extrapolation. In some systems (e.g. seeds with prolonged or unpredictable dormancies) this is challenging because seeds can germinate or be ingested after many years in the seed bank (Bonis et al. 1995, Malo et al. 1995, Jaroszewicz et al. 2008).

Seed germination, the second sub-component of quality, is most often estimated by means of field (sometimes greenhouse) experiments, in which either defecated/regurgitated or depulped seeds are planted at marked spots, often protected from seed and seedling predation and ideally also distributed across the range of relevant microhabitats (Hollander and Vander Wall 2004, Culot et al. 2017, Neghme et al. 2017). Intact seeds or seeds with pulp are usually planted as controls or to simulate other dispersal treatments (dropped or unconsumed fruits; Robertson et al.

2006). Seeds dispersed by larger mammals are customarily planted within dropping piles to incorporate the conditions of the substrate (Cosyns et al. 2005b, Milotić and Hoffmann 2016). Germination of seeds dispersed by scatter-hoarders is often measured as part of the seed-fate tracking outlined in the previous paragraph, using marked seeds offered under mother trees or marked at caches (Jansen et al. 2004). Similar to post-dispersal seed predation, seed germination is usually expressed as a frequency (seeds germinating per seed deposited), hence they are directly amenable for SDE calculations. However, precaution should be taken to obtain reliable estimates that span the complete duration of seed viability (Robertson et al. 2006). For long-lived seeds with prolonged dormancies, long-term field setups combined with standard assays such as Tetrazolium Testing might be an adequate method to assess seed germination, mortality and viability (Pace et al. 2016).

The probability of seedlings becoming adults, the third sub-component of quality, is rarely measured. In most cases, this assessment is limited to seedling establishment, i.e. seedling-to-sapling survival in trees. The most common method involves the repeated inspection of marked seedlings, emerging from germination experiments or localised in field surveys, noting the proportion of those alive and dead to build survival curves (Hollander and Vander Wall 2004, Garcia et al. 2005). Seed survival is usually expressed as a frequency (seedlings reaching sapling stage per seedling marked), hence they are directly amenable for eSDE calculations.

## An application of the eSDE framework

### Data collection

To illustrate the usefulness of our proposed extension and the kind of insights that can be gained from the eSDE framework, we searched published literature that reported suitable data for either of the four prominent plant–disperser interaction types: frugivores, folivores, scatter-hoarders and granivores. We started by searching the ISI Web of Science using combinations of ‘SDE’ and ‘frugivor\*’, ‘scatter-ward\*’, ‘herbivor\*’ or ‘granivor\*’. To date, no study provided all information necessary to calculate all eSDE metrics, but for 60 studies we were able to find a solid basis of partial information. For studies presenting at least two of the five eSDE metrics, we searched for complementary studies with the information necessary to calculate complete eSDE metrics. We continued searching until each of the four plant–disperser interaction types was represented by at least five interaction pairs, with the longest search required for granivores and folivores because field data for the quality component has been rarely assessed in these plant–disperser interaction types.

Although no study included all necessary information, some studies included useful data for multiple plant–animal interactions. In total, data were extracted from 25 studies (initial and supporting studies, Supporting information), converted to the same units and processed according to the

methods and formulas provided in Table 1. This provided estimates for eSDE quantity (53) and quality (47), leading to 47 complete estimations of extended Seed dispersal effectiveness. We were not always able to obtain estimates of all quality subcomponents because for some interaction types (mostly for folivores), quality was measured as single, aggregated data (e.g. by sowing seeds in dung and assessing seedling establishment). Of the quality component, 30 interaction pairs included differential seed deposition (i.e. they combined estimates measured separately in different microhabitats). The dataset (Supporting information) consisted of 23 different animal species dispersing 19 different plant species from temperate and tropical areas. Frugivores included frugivorous birds and lizards from temperate and Mediterranean regions of Europe and tropical regions in South America; scatter-hoarders included small mammals from semiarid areas of North America and Mediterranean areas of Europe; granivores included waterbirds from Mediterranean regions of Europe; and folivores included large ungulates (cattle, horses) from temperate regions of Europe.

### Illustrative results

Our first comparison with the thus far available data suggested that frugivores, folivores, scatter-hoarders and granivores all contributed to seed dispersal. We found large variation among the four prominent plant–disperser interaction types and more so along the quantity axis (mean  $0.18 \pm 0.24\text{SD}$ ) than along the quality axis (mean  $0.08 \pm 0.08\text{SD}$ , Fig. 3, 4). This suggests that vertebrate species may differ more in the number of seeds they deposit away from the mother plant, than in the effects such dispersal processes have on seed fate. Overall, the most efficient dispersers in our dataset were scatter-hoarders, followed by frugivores, granivores and folivores. All groups (except perhaps granivores) showed a wide range of eSDE, and interaction types traditionally considered as highly efficient included interaction pairs emerged as fairly inefficient interactions, for example the frugivores *Turdus pilaris* for *Ilex aquifolium* and *Turdus philomelos* for *Crataegus monogyna* (Martínez et al. 2008, Morales et al. 2013). This low effectiveness was directly related to the low germination rates of seeds after deposition, and contrasts with e.g. the relatively high dispersal quality provided by granivorous waterbirds, which included moderately high germination rates after deposition (Fig. 4, Supporting information). Although these observations require much further exploration, they suggest that some animal dispersers that provide a harsher treatment in the gut such as avian granivores, may be more effective in breaking seed dormancy – thus compensating their low dispersal quantity with a higher dispersal quality.

Variation in quantity was present in both removal and deposition, with folivores and granivores showing a low quantity mostly due to their surprisingly low removal rates (< 20% in most interactions) in comparison to frugivores and scatter-hoarders. However, for some interaction pairs, low removal rates were compensated by relatively high deposition rates (Fig. 4). High dispersal quantity among frugivores

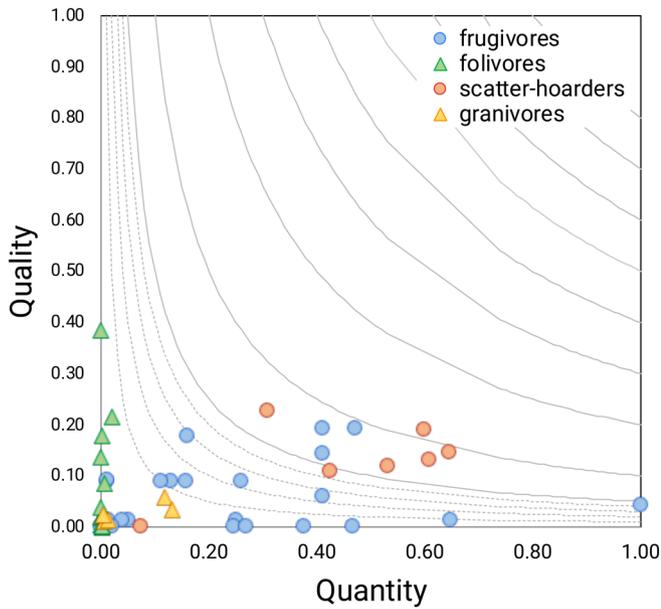


Figure 3. Extended seed dispersal effectiveness (eSDE) calculated for 47 plant–disperser interactions of four interaction types. Filled circles indicate interactions of frugivores and scatter-hoarding granivores with woody plant species, and filled triangles indicate interactions of folivores and non-hoarding granivores with non-woody plant species. Isoclines represent lines of equal eSDE.

resulted largely from high deposition rates, as in these species seeds were rarely destroyed during the dispersal process. In contrast, high dispersal quantity among scatter-hoarders was mostly driven by high removal rates. When such patterns are taken together, different vector types clearly occupied distinct regions of the parameter space defined by deposition and removal probabilities (Supporting information). Altogether, the highest quantity values were found for scatter-hoarders, followed by frugivores, with folivores and granivores showing the lowest scores.

Dispersal quality showed a general trade-off between its different subcomponents, leading to contrasting patterns for different interaction types (Fig. 4). Frugivory came with moderate post-dispersal predation rates, highly variable germination probabilities (with the broadest variation among interaction pairs) and high establishment probabilities. In contrast, granivores and scatter-hoarders provided high escape from post-dispersal seed predation, and moderate germination and establishment success. High escape from post-dispersal seed predation may reflect an understudied subcomponent, or could be because deposited seeds already escaped a predatory interaction once hidden in caches. The quality component for folivores was mostly assessed as aggregated data, making comparative information on subcomponents very scarce. Altogether, the highest quality values were found for scatter-hoarders, followed by frugivores, with folivores and granivores showing the lowest scores.

An example of patterns that could be derived using the eSDE framework is a difference in effectiveness between

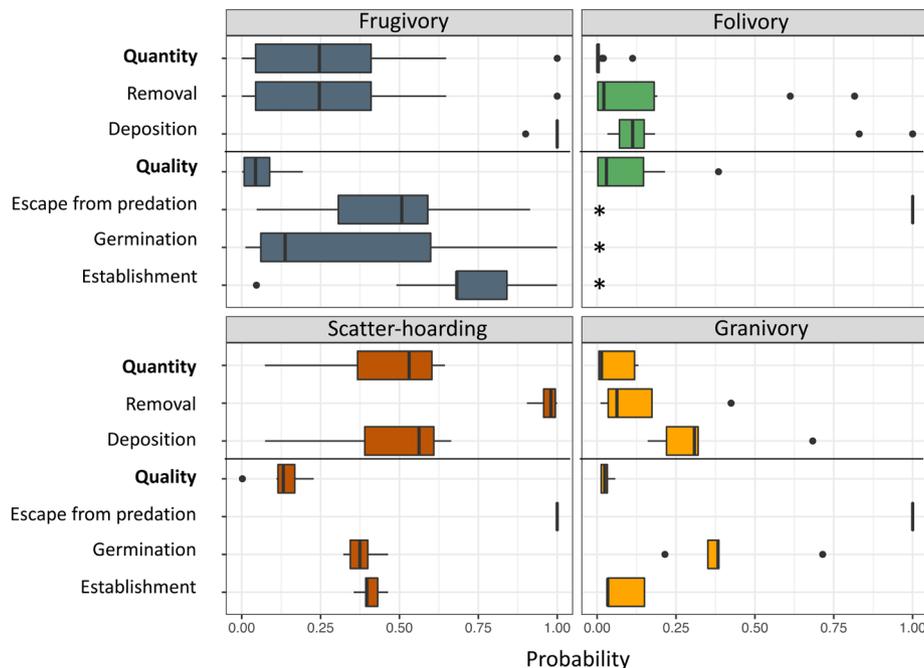


Figure 4. Seed dispersal quality and quantity and their components for the four plant–disperser interaction types, based on data from the literature. See the Supporting information for a visualisation as effectiveness isoclines. Asterisks at the quality components of folivores indicate missing information, because quality is generally assessed directly without separately assessing its subcomponents.

woody and non-woody plant species. Our limited dataset indicated the highest effectiveness for woody species dispersed by scatter-hoarders (Fig 3), which may be driven by the generally larger seeds of woody plant species following the dichotomy proposed by McKey (1975). For woody plants the variation was larger for the quantity component than for the quality component, while for non-woody plants the opposite was true. Yet, non-woody plants were dispersed by granivores and folivores, hence the currently available data does not allow drawing clear conclusions on this particular contrast. However, it still exemplifies the potential for further exploration of interactions and their evolutionary underpinnings across a broad range of plant–animal interactions.

Overall, our results provide a first illustration that, with a limited redefinition and extension to ensure the coherence of the estimated metrics, we were able to collate data allowing for a broad comparison across interaction types ranging from pure mutualisms to predominantly antagonisms (Gómez et al. 2019), and including data from different biomes and broadly different mutualistic partners (from herbs to woody plants, from mammals to birds). At this stage, the value of these comparisons is mostly to generate insights into general ecological and evolutionary patterns across systems, because detailed data on local variability are not yet available. However, the eSDE framework can reduce the noise introduced by methodological variability across the different study systems, and will hopefully stimulate the collection of more complete and comparable data. Together, this would allow more generalisation and testing of broad as well as more specific ecological and evolutionary patterns.

## Future applications and emergent issues

A consistent standardisation of all SDE components and subcomponents in the eSDE framework allows assessing and comparing seed dispersal effectiveness across a broad range of species, biomes and geographic areas. This can strongly advance 1) our fundamental insights into the ecology and evolution of plant–animal interactions, 2) our ability to draw raw predictions on plant dispersal and recruitment, with consequences for plant diversity maintenance and regulation (Nathan and Muller-Landau 2000) and 3) our ability to provide science-based advice on conservation and restoration of plant–animal interactions.

Systematic assessment of eSDE across a larger range of plant- and animal species allows to test hypotheses about the (co)evolution of seed dispersal mutualisms, including conditional mutualisms. Such hypotheses include the relative importance of facilitation traits versus exploitation barriers, the effect of cheating on the evolutionary stability of mutualistic relationships, or the assessment of the impacts of species loss on (mutualistic, antagonistic and mixed) ecological networks (Albrecht et al. 2018, Sebastián-González et al. 2020, Cao et al. 2022). Systematic metrics will allow for comparisons among ecological systems – including those present in different ecosystem types (e.g. terrestrial versus freshwater versus

marine) and biomes (e.g. tropical versus temperate versus Mediterranean); and for a broad-scale evaluation of the influence of different plant and vector traits, including comparisons among plant and/or animal functional groups (Dennis and Westcott 2006, Aslan et al. 2019). The eSDE framework further facilitates the inclusion of other seed dispersal mechanisms such as epizoochory, dyszoochory, or even hydrochory or anemochory. Both quantitative and qualitative components can be included, using for example estimates of dispersal quality for wind (Soons et al. 2017). This would pave the way for comparing or combining dispersal mechanisms. The use of dimensionless quantity and quality metrics, directly amenable to transition probabilities between well-defined demographic phases, will hopefully facilitate the calculation of SDE for mixed dispersal systems, in particular those involving diplochory (secondary dispersal) by different combinations of animal and non-animal vectors. The dimensionless estimates in the framework have the advantage that they can be multiplied when different dispersal vectors operate subsequently on the same seed (i.e. to estimate the joined impact of primary and secondary dispersal). This allows an estimation of the joint quantity and quality component of the ensemble (which are respectively equal to the quantity component of the first vector, and the weighted average of the quality components of the first and second vector; with the quality component of the second vector being used as weighting factor).

If data are available to include differential deposition, effectiveness can be compared among dispersal distances in heterogeneous landscapes. The inclusion of dispersal distance estimates could be further expanded by treating distance as a continuous variable, even if dispersal probability and fate is not isotropic (i.e. they vary with direction from the mother plant). In such case, one-dimensional curves for the quantity and quality (sub)components could be derived from spatially explicit models (Santamaría et al. 2007). Assessing the contribution of different dispersal mechanisms, their potential interactions and the inclusion of dispersal distance are important next steps for our understanding of ecosystems.

The value of an improved understanding of seed dispersal is illustrated by the wide range of relevant plant–disperser interactions presented here, which emphasises the dependence of plants on a wide range of vertebrate animals. More than half of all woody plants are dispersed by vertebrates (Rogers et al. 2021) and a potentially similar number for non-woody plants, which makes it important and urgent to study how these (complex) interactions are affected by human impact (Fricke et al. 2022). Anthropogenic stressors such as climate change, landscape fragmentation and the introduction of alien species will require a fully functional dispersal capacity for plants to respond with range shifts and sufficient connectivity for survival. However, the on-going animal and population loss from ecosystems (defaunation) has far reaching consequences on such dispersal capacity (Carvalho et al. 2016). It is paramount to understand the effective role of each disperser type and the generalities within and across plant dispersal systems if we want to understand and halt the consequences of dispersal disruptions on a global

scale (Fricke et al. 2022). The extended framework can inform on the need, design and impact of biodiversity protection and ecosystem restoration – especially, when it involves rewilding and/or the reintroduction of locally-extinct species.

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**Casper H. A. Van Leeuwen** and **Nacho Villar** contributed equally to this publication. **Casper H. A. Van Leeuwen**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Nacho Villar**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Irene Mendoza Sagrera**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Andy J. Green**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Elisabeth S. Bakker**: Conceptualization (supporting); Funding acquisition (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Merel B. Soons**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Mauro Galetti**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Patrick A. Jansen**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Bart A. Nolet**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Luis Santamaría**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

### Data availability statement

All data presented in the manuscript is available in the Supporting information.

### Supporting information

The Supporting information associated with this article is available with the online version.

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