Passive external transport of freshwater invertebrates by elephant and other mud-wallowing mammals in an African savannah habitat

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SUMMARY

1. Recent findings hint at the potential importance of mammals affecting the spatial dynamics of aquatic organisms in areas where mammals live in close association with water. Perhaps the most iconic example of such an environment is the African savannah.
2. We investigated dispersal patterns of freshwater organisms among a set of temporary ponds in SE Zimbabwe to test the hypothesis that large mammals, and particularly African elephants (*Loxodonta africana*), can be important vectors of aquatic organisms. Dispersal kernels were reconstructed by hatching mud collected from 'rubbing' trees located at increasing distances from a set of isolated ponds. To assess the relative importance of other mammalian vectors, the vertical distribution of mud on rubbing trees was mapped and related to the body size of candidate vector species.
3. Laboratory hatching of mud samples revealed large numbers of propagules of 22 invertebrate taxa as well as some aquatic macrophytes. Dispersing communities reflected source communities and diverged with increasing distance from the source. Both dispersal rates and richness of transported taxa decreased significantly with dispersal distance. No indications for differences in dispersal capacity among propagule types were detected. Instead, common propagules were more likely to travel greater distances. Most mud was attached to trees at heights >1.5 m, implicating elephants as the dominant vector. Vertical distributions of tree mud, however, also revealed clustering at heights up to 50 cm and 90–120 cm corresponding to the height of warthog, rhinoceros and buffalo, respectively. Finally, variation in the vertical distribution of mud on trees in combination with differences in vector vagility suggests that local differences in vector species composition may affect passive dispersal dynamics of aquatic organisms.
4. Based on vagility and vector load, mud-wallowing mammals emerge as highly effective vectors that, in some areas, may be more important in transporting aquatic organisms than traditionally recognised vectors such as waterbirds. Since most large- and medium-sized mammals currently have restricted geographic distributions, it is likely that mammal-mediated dispersal was more important in the past.

Keywords: aquatic invertebrates, dormant propagules, ecto/epizoochory, passive dispersal

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Introduction

Vector-mediated transport has fascinated naturalists since Aristotle and Theophrastus (Thanos, 1994). First recognised in plants, vector-mediated transport was later also adopted to explain wide distribution patterns of small aquatic animals and microorganisms (Hudson & Gosse, 1886). Darwin (1859) was among the first to report adherence of freshwater invertebrates to animal vectors in a now-classic experiment in which he briefly submerged a severed duck's foot in an aquarium and monitored viability of aquatic organisms attached. Inspired by Darwin's pioneer work, and propelled by productive ornithological research groups, current literature related to vector-mediated dispersal of freshwater organisms considers waterbirds as the most important natural dispersal vectors (Frisch, Green & Figuerola, 2007; Green *et al.*, 2008; Brochet *et al.*, 2010a) responsible for colonisation and exchange of propagules among isolated unconnected freshwater habitats. Man undoubtedly remains unrivalled when it comes to transporting vast numbers of exotic organisms including many freshwater invertebrates on a global scale (Havel & Shurin, 2004; Green *et al.*, 2005; Jacobs & Mac Isaac, 2007; Waterkeyn *et al.*, 2010a,b). Still, waterbirds firmly hold the second place in the vector hall of fame and are held responsible for most long-distance dispersal events of freshwater invertebrates for which humans cannot be blamed (Brendonck, Thiery & Coomans, 1990; Figuerola, Green & Michot, 2005; Green & Figuerola, 2005; Muñoz *et al.*, 2008). It cannot be denied that very few organisms that visit ponds and lakes cover such great distances as migratory waterbirds and a considerable number of studies report aquatic organisms adhering to plumage or surviving ingestion (reviewed in Charalambidou *et al.*, 2005).

There are, however, several lines of evidence that support a more pluralistic view with different vectors operating at different scales. At local scales, such as within dense clusters of temporary pool habitats, wind has been shown to be the dominant dispersal agent (Vanschoenwinkel *et al.*, 2008a). Besides birds, a number of other animal vectors are known to transport propagules. Amphibians have since long been identified as effective vectors, be it on relatively local scales (Bohonak & Whiteman, 1999; Lopez, Rodrigues & Rios, 1999; Vanschoenwinkel *et al.*, 2008b). Additionally, both water bugs such as *Notonecta* (Van De

Meutter, Stoks & De Meester, 2008) and water beetles (Beladjal & Mertens, 2009) as well as certain mammal species are likely to be important dispersal vectors at local to regional scales that have been historically overlooked (but see Peck, 1975). Two recent case studies investigated the potential of mammals for transporting aquatic organisms. Vanschoenwinkel *et al.* (2008c) investigated faeces and mud samples from the coats of wild boars in a Mediterranean wetland area and found that these contained considerable numbers of zooplankton propagules that hatched upon inundation. In the same study area, Waterkeyn *et al.* (2010a,b) recovered both propagules and live freshwater invertebrates from the fur of nutria (*Myocastor coypus*; Molina, 1782), an aquatic rodent introduced to southern France. The feasibility of other mammal species as vectors as well as the potential importance of mammal-mediated dispersal in other habitat types and in other parts of the world, however, have thus far not been investigated.

Perhaps the most striking example of a habitat where large numbers of different mammal species live in close association with lentic water bodies is the African savannah. In these dryland areas, movement of mammals is strongly linked to availability of surface water (Redfern *et al.*, 2003; Loarie, Aarde & Pimm, 2009) and many species often migrate over long distances to drink (Owen-Smith, 1992). While visiting waterbodies, mammals can come into contact with drought-resistant life stages of plants and invertebrates that may adhere to fur, feet or hooves (Thiéry, 1987). Propagules can also be ingested while drinking or grazing aquatic vegetation, potentially resulting in internal transport if they can survive digestion (Charalambidou *et al.*, 2005; Vanschoenwinkel *et al.*, 2008c). Additionally, many African mammal species, such as warthog, rhinoceros, buffalo and elephant frequently engage in wallowing, purposely covering their skin with mud from shallow freshwater habitats (Wright & Luck, 1984; Owen-Smith, 1992), an activity that could potentially result in the attachment of large numbers of propagules present in the sediment (Vanschoenwinkel *et al.*, 2008c). Acquiring and maintaining a protective cover of mud is beneficial for these largely hairless mammals since it protects against sunburn, helps to disinfect wounds and traps parasites such as ticks or fleas (Sardin & Cargnelutti, 1987; Fernandez-Llario, 2005). To get rid of these ectoparasites embedded in mud, mud-wallowing

mammals often rub themselves against trees (Sardin & Cargnelutti, 1987; Owen-Smith, 1992). As a result of such rubbing behaviour, sediment depositions can often be located on the trunks of trees located at different distances from potential source habitats, providing opportunities to sample the propagule content of these depositions and reconstruct dispersal patterns (Vanschoenwinkel *et al.*, 2008c).

In this study, we investigated the potential of large mammals as dispersal vectors of freshwater invertebrates in the African savannah. The research took place in the Malilangwe Wildlife Reserve, a conservation area in the lowveld of Zimbabwe that is home to large numbers of indigenous mammal species and encompasses more than 300 temporary ponds as well as several permanent dams (Fig. 1). Mud-wallowing mammals in the area include Cape buffalo [*Syncerus caffer caffer* (Sparrman)], warthog [*Phacochoerus africanus* (Gmelin)], white rhinoceros [*Ceratotherium simum* (Burchell)], black rhinoceros [*Diceros bicornis* (Linnaeus)] and African bush elephant [*Loxodonta africana* (Blumenbach)]. We hypothesised that mud-wallowing mammals, and particularly elephants, would be important vectors for dispersal of freshwater invertebrates in the study area. We decided to focus on external rather than internal transport, since previous research on wild boar in Europe suggested that external transport is likely to be more important in terms of number and diversity of propagules transported than internal transport (Vanschoenwinkel

et al., 2008c). First, we quantified propagule content and reconstructed dispersal kernels using mud collected from a set of rubbing trees located at increasing distances of temporary ponds that are regularly visited by elephants. Based on their size, abundance and pronounced wallowing behaviour, we expected that elephant would be the most important mammalian vector in the area. Second, to assess the relative importance of other mammalian vectors, the vertical distribution of mud on rubbing trees was mapped and related to the body size of candidate vector species.

Methods

Study area

The study was carried out in the Malilangwe Wildlife Reserve, a 40 000-ha privately owned nature reserve in SE Zimbabwe (Fig. 1). This region, which is bordered by the Chiredzi and the Runde rivers, consists mainly of largely pristine savannah habitat (lowveld) and contains more than 300 temporary and several permanent ponds or pans as they are locally referred to. Local vegetation is Mopane (*Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Léon) and mixed *Acacia/Combretum*-wooded savannah. Malilangwe houses large natural populations of indigenous large mammal species, several of which frequently wallow in the mud of temporary ponds.
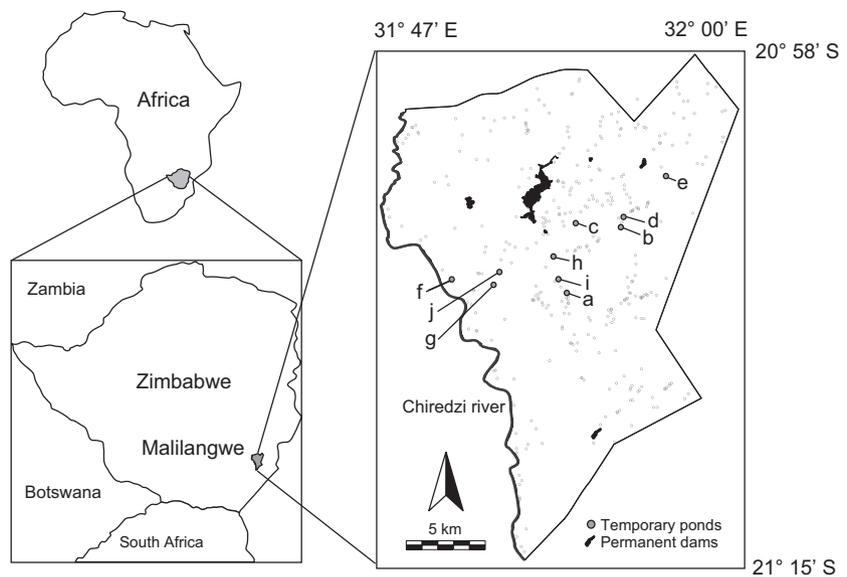

Fig. 1 Location of the study area: the Malilangwe Wildlife Reserve in SE Zimbabwe. All temporary (grey) and permanent waterbodies (black) are indicated. Temporary pond localities used in this study are labelled (a)–(j).

Quantifying elephant-mediated dispersal

The study area was visited first in November 2009 at the end of the dry season when, with the exception of a small number of permanent water bodies, all ponds were dry. For five typical temporary ponds known to be frequented by elephants, dry mud was sampled both from the pond as well as from five trees situated at increasing distances (pond a: 68, 89, 107, 256 and 394 m; pond b: 66, 86 and 109 m; pond c: 28, 136, 150 m, 178 and 260 m; pond d: 86, 107, 120, 275 and 331 m; pond e: 10, 40, 66, 93 and 153 m). For pond b, only three rubbing trees could be located. For each pond, ten circular sediment samples (diameter 5 cm, depth 3 cm) were obtained, five in the littoral zone and five in the deeper parts. Collected sediment was broken up and homogenised, and a subsample of 200 g was isolated for hatching. Rubbing trees were located up to 400 m from the nearest pond; although rubbing trees can sometimes be found further away, none were available. To restrict the experiment to elephant-mediated dispersal, mud was collected at heights >1.5 m. Dry mud was removed from trees making use of a metal spatula, a rigid brush and a set of fine tweezers. Loose sediment particles were collected in a plastic ziplock bag. Average weight of collected tree mud samples was 90 ± 31 g. However, exceptionally, some trees directly adjacent to ponds held large amounts of sediment, sometimes exceeding several kilograms. For these, sample weight was limited to *c.* 100 g, and the total sediment load (g) was estimated by extrapolating the weight of mud collected from three quadrants of 100 cm^2 to the entire mud coverage (cm^2) on each tree. Sediment coverage was measured to the nearest 25 cm^2 by placing a graduated transparent plastic sheet (5-cm grid) over the tree trunk. In case not all sediment was sampled, estimated propagule densities (propagules 100 g^{-1} sediment) and sediment load (g) were used to estimate the total propagule content of the sediment attached to each rubbing tree.

All samples were dried and stored in the dark at room temperature and processed in the laboratory in March-April 2010. After weighing, individual samples were transferred to 1.5-L aquaria that were filled with EPA medium (Anonymous, 1985; conductivity 20 μS cm^{-1}) and incubated at 17 °C under a 14 h light/10 h dark regime. In the following 24 h, the temperature was gradually increased to 25 °C. All experimental conditions were selected to maximally mimic natural conditions after rains. During the first 2 days, a small inoculum (*c.* 20 million cells per aquarium) of the green alga *Scenedesmus obliquus* (Turpin) Kützing was added as food for hatching organisms. During the entire experiment, each aquarium was covered by a lid and supplied with filtered air through individual tubes. Three aquaria were set up as controls to test for contamination in the incubators. All aquaria were sampled on six successive occasions: 4, 8, 11, 15, 19 and 23 days after inundation. Next, the medium of each aquarium was carefully decanted and filtered over a 64-μm filter. Hatched organisms were isolated, identified and counted under a stereomicroscope and stored in 70% ethanol. Larvae and juveniles of large branchiopods were isolated and cultured until they reached maturity to allow for species identification. Organisms and propagules smaller than 300 μm were examined under a higher-resolution microscope. To complete the species list and to evaluate hatching success, the presence of any unhatched propagules after the hatching experiment was checked; a subsample of 20 g of mud was collected from each aquarium, sieved over a 125-μm mesh and subjected to 3 min of density centrifugation (sugar floatation method; Onbé, 1978; Marcus, 1990), a standard method to isolate invertebrate propagules from sediment. Sediment was first rinsed and sieved and then transferred to a 25-mL falcon tube to which a 1 : 1 sacharose solution was added up to a total volume of 20 mL. After vigorously homogenising by shaking, the tubes were centrifuged for 3 min at 1512 *g*. After this, the lighter fraction, which typically contains organic material, was decanted and any propagules present were identified and counted using a dissection microscope. Afterwards, another 10 min of density centrifugation was applied as an additional measure to check the efficiency of the method. For 5% of all collected samples, the residue that remained after these two rounds of centrifugation was checked for the presence of remaining propagules under a dissection microscope. This final control, however, yielded no additional propagules. Only propagules that were deemed viable were included in our analysis: anostracan and spinicaudatan resting eggs when a clear embryo popped out when squeezed (method cf. Brendonck & Riddoch, 2000); cladoceran ephippia when they contained intact eggs without external

signs of degradation. For some taxa (e.g. bryozoan statoblasts), viability could not be verified from external structure.

Species identification

All hatched organisms were identified using available literature (large branchiopods to species level: Hamer, 1999; Cladocera to species level: Seaman, Kok & Watson, 1999; Flößner, 2000; Rotifera (with exception of bdelloid rotifers) to genus level: Ruttner-Kolisko, 1974); Copepoda to order level. Unhatched invertebrate propagules were counted and identified where literature was available (for Cladocera: Flößner, 2000; Vandekerkhove *et al.*, 2004; for large branchiopods: Brendonck & Coomans, 1994a,b; and for Bryozoa: Tachet *et al.*, 2000).

Inferring relative importance of different vector species from mud patterns on rubbing trees

To identify different vector species and test the hypothesis that dispersal dynamics depend on local availability of vectors, vertical distribution (height, vertical range and thickness in mm) of mud on rubbing trees ($n = 60$) was mapped during a second visit to the study site in January 2010. Based on long-term observations by local wildlife managers, five ponds (ponds f, g, h, i and j) were selected that are known to be frequented by different assemblages of large mammals. Identity of visiting mammals was confirmed by a professional wildlife tracker based on the presence of specific foot prints near ponds and rubbing trees and based on different hair types present in the mud attached to individual trees. At each pond location, 12 rubbing trees were selected at different distances from the source pond (0–100 m). For each tree, the maximum thickness of sediment was measured from ground level up to the maximum height of sediment cover, each time at 10-cm intervals using the depth probe of a common vernier caliper (0.5-mm accuracy).

Data analyses

Distances between individual trees and the nearest pond were calculated in ArcGIS (V8.1, ESRI, Redlands, CA, U.S.A.). Distances of each tree to the nearest pond were always much shorter than dis-

tances to other ponds in the area. This allows for the reconstruction of clear dispersal kernels without strong interference by other sources as well as to study the link between the dispersing and source communities. Relationships between distance to source habitats and sediment load (kg), propagule content, propagule density and richness of dispersing propagules, respectively, were investigated using regression models. We note that because not all sediment could be collected for a few trees that were in the immediate proximity of source ponds, estimates of taxon richness present in tree mud samples at short dispersal distances are likely to be underestimated. The effect of dispersal distance on sediment load, propagule density, propagule content and richness of tree mud samples, including hatched and unhatched propagules, was analysed using the PROC MIXED procedure using SAS/STAT software (V9.1, Statsoft Inc., Tulsa, OK, U.S.A.). Dispersal distance, propagule content, propagule density and sediment content (kg) were log transformed to comply with the model assumption of a normal error distribution, verified using a Shapiro Wilk's test. To investigate effects of dispersal distance, while correcting for differences related to the identity (species composition, propagule density) of the nearest dispersal source, source pond was included as a random factor in the models. In analyses of propagule content and propagule density, only macrozooplankton taxa were included since the mesh size used (64 μm) during sampling of the aquaria did not retain most rotifer propagules. High reproduction rates of rotifers in the aquaria may also have led to less reliable estimates of the number of hatched propagules.

To test whether species composition of invertebrates hatching from tree mud reflected species composition of the nearest source ponds and whether the difference between species composition of pond and tree mud increased with distance from the nearest source, we used a combination of analyses. First, we tested whether the richness and density of propagules of the nearest source pan are good predictors of the richness and propagule density of tree mud samples using linear regression models. Because the source ponds are the independent units in these analyses, for each pond we summed propagule content of the different adjoining rubbing trees to provide a single sample. Secondly, an unpaired *t*-test was performed to test for differences between richness and propagule

density of invertebrates hatching from pond sediment compared to tree mud samples. Additionally, to detect potential differences in dispersal capacity, the relationship between the relative abundance of species in the dispersing community and their relative abundance in pond sediments was investigated using linear regression models. Finally, to detect underlying factors responsible for differences in dispersal distance distributions among propagule types, a multiple regression model was constructed with the maximum dispersal distance of each propagule type as the response variable and with propagule size (μm) and propagule abundance (i.e. total number of propagules of this type found in pond sediment) as predictor variables.

Non-metric multidimensional scaling (MDS) based on Bray Curtis dissimilarity indices implemented in PRIMER (V5, Primer LTD., Plymouth, U.K.) was applied to visualise differences in species composition of invertebrate taxa found in pond and tree mud samples. Additionally, a regression model was used to explicitly test whether community dissimilarity increased with increasing distance from presumed source ponds. Note that since only the differences between each tree and its respective nearest source pond are retained in this analysis rather than the complete reciprocal distance matrices, this relationship could not be analysed using Mantel correlations. Since only the difference in community composition of each tree and its nearest source pond are used as observations, these can be considered independent. All linear regressions were performed using PROC REG and *t*-tests using PROC TTEST in SAS/STAT software.

Results

A total of 1947 invertebrate propagules, belonging to 23 different taxa were encountered in the tree mud samples (Table 1), with, on average, 75 ± 82 propagules (0.6 ± 0.7 propagules g^{-1}) and 7 ± 2.6 taxa per sample. Conversely, mud samples from presumed source ponds contained on average 166 ± 0.5 propagules (1 ± 0.4 propagules g^{-1}) and 10 ± 1.5 taxa. We also observed some plants germinating from tree mud, including *Lemna* sp., at least two unidentified macrophytes and the colonial chlorophyte *Volvox* sp. No propagules were detected in control aquaria.

A significant negative relation was found between taxon richness of invertebrates present in tree mud

samples and dispersal distance ($F_{1,21}$ = 8.8; P = 0.008; Fig. 2a). Propagule content significantly decreased with increasing dispersal distance ($F_{1,21}$ = 28.91; P < 0.001; Fig. 2b).

Both propagule density ($F_{1,21}$ = 4.61, P = 0.04; Fig. 2c) and total weight ($F_{1,21}$ = 13.25, P = 0.001; 2d) of sediment attached to rubbing trees decreased significantly with dispersal distance.

Propagule density of tree mud samples was not positively related to the propagule density in the nearest potential source habitat (β = −P = 0.41, r^2 = 0) and neither was taxon richness (β = 0.21, P = 0.60, r^2 = 0). Taxon richness (unpaired *t* test; t = −2.31, P = 0.03) but not propagule density (unpaired *t* test; t = −0.59, P = 0.55) was significantly higher in the pond sediments (10 ± 1; n = 5) than in the tree mud samples (7 ± 3; n = 23). Overall, we did not find a significant relation between propagule richness in tree mud samples and the richness of propagules detected in the nearest source pond (β = 0.16, P = 0.74, r^2 = 0). Some taxa retrieved from tree mud were absent in the sediment of the nearest source habitat, including a number of rotifer taxa (*Euchlanis*, *Hexarthra*, *Conochilus* and *Filinia*) and aquatic macrophytes. The abundance of taxa in pond sediments was generally a good predictor of their abundance in tree mud samples (β = 2.65, P < 0.001, r^2 = 0.96). Log-transformed propagule abundance in source ponds (β = 94.26, P = 0.03) but not propagule size (β = −0.07, P = 0.67) was a good predictor of maximum dispersal distance of different propagules (multiple linear regression, $r^2_{adj.}$ = 0.26).

As visualised in the MDS plot, communities hatching from sediment from different ponds were quite similar, while species composition of communities hatching from tree mud samples was variable (Fig. 3a), with community dissimilarity increasing significantly with increasing distance from the nearest dispersal source (β = 0.09, P = 0.005, r^2 = 0.31; Fig. 3b).

The upper limit of mud coverage on individual trees ranged from 40 to 380 cm above ground level. Overall, comparison of mud patterns on the studied tree trunks revealed that mud is not homogeneously distributed along tree trunks and that thickness of mud on the trunks peaked at heights of 0–50, 90–120 and 140–290 cm above ground level (Fig. 4a,b), roughly corresponding to the height of the flanks and shoulders of warthogs, rhino or buffalo and elephant, respectively (Fig. 4c). Tree mud patterns

Table 1 List of invertebrates present in mud samples collected from rubbing trees and ponds. Both total number and % occurrence of propagules are shown. Taxa for which the number could not be reliably quantified are indicated by +

	Taxa	Tree mud samples ($n = 26$)		Pond mud samples ($n = 5$)	
		No.	% samples	No.	% samples
Hatched propagules					
Cladocera	*Moina belli*	163	38.5	26	100
	Ceriodaphnia quadrangula (O.F. Müller)	9	23.1	3	20
	Macrothrix spinosa Sars	17	7.7	1	20
	Alona sp.	6	11.5	2	20
	Leydigia macrodonta Sars	25	15.4	3	40
	Daphnia sp.	0	0	1	20
Notostraca	*Triops granarius* Lucas	2	7.7	0	0
Anostraca	juv.	22	30.8	1	20
	Branchipodopsis wolfi Daday	6	7.7	0	0
	Branchinella ondonguae Barnard	1	3.8	1	20
	Streptocephalus bidentatus*	8	11.5	7	80
	Streptocephalus cafer (Lovén)	2	7.7	1	20
	Streptocephalus juv.	38	38.5	16	60
'Conchostraca'	juv.	2	3.8	8	60
	Leptestheria striatoconcha Barnard	0	0	5	60
	Cyzicus australis (Lovén)	0	0	8	40
Copepoda	*Calanoida* sp. (nauplius)	4	7.7	7	80
Ostracoda	spp.	1182	96.2	408	100
Rotifera	*Asplanchna* sp.	+	19.2	+	40
	Brachionus sp.	+	84.6	+	40
	Euchlanis sp.	+	15.4	0	0
	Hexarthra sp.	+	30.8	0	0
	Conochilus sp.	+	15.4	0	0
	Filinia sp.	+	26.9	0	0
Other taxa	*Volvox* sp.	4	3.8	0	0
	Lemna sp.	6	11.5	11	40
	Macrophyte (monocot)	8	15.4	0	0
	Macrophyte (dicot)	1	3.8	0	0
Unhatched propagules					
Cladocera	*Moina* sp.	63	53.8	14	100
	Ceriodaphnia sp.	14	38.5	6	60
	Alona sp.	1	3.8	0	0
	Chydoridae spp.	6	23.1	1	20
	Daphnia sp.	1	3.8	0	0
Notostraca	*Triops granarius* Lucas	14	42.3	2	40
Anostraca	*Streptocephalus bidentatus**	241	65.4	21	100
	Branchipodopsis sp.	87	46.2	8	100
Bryozoa	*Plumatella* sp.	29	42.3	2	20

*Hamer & Appleton.

also reflected composition of local vector species assemblages (Fig. 4a). Mud patterns on the trunks of trees sampled near ponds f and g, which were not visibly visited by elephants, ranged from 0 to 110 cm above ground level. In ponds f and i, which were mainly visited by warthogs, most tree mud was attached below 60 cm. On the bark of trees in the proximity of pond g, pronounced deposition of mud was observed at a height of 90–110 cm, corresponding to the shoulder height of rhino and buffalo. Long-term observations in combination with the inspection of the area for tracks and hairs embedded in tree mud indicate that this pond is used by warthog and white rhino, while no traces of buffalo were found. Presence of elephants and warthogs was confirmed at pond h while tracks of all four potential vector species were observed near pond i, where mud reached heights from ground level up to 380 cm, but predominated at
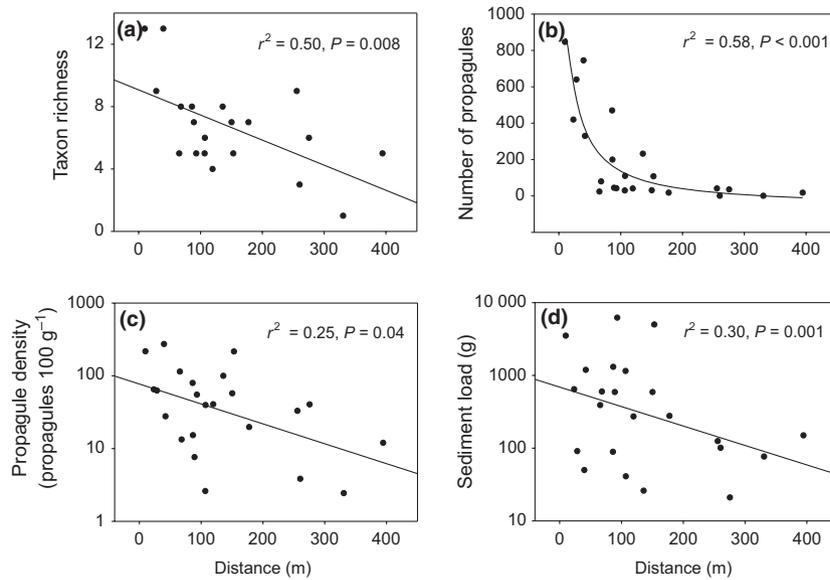
Fig. 2 Relationships between dispersal distance (distance to nearest pond) and (a) richness, (b) propagule content (inverse second-order polynomial fit), (c) propagule density of freshwater invertebrates hatching from sediment collected from rubbing trees and (d) total amount of sediment attached to rubbing trees.
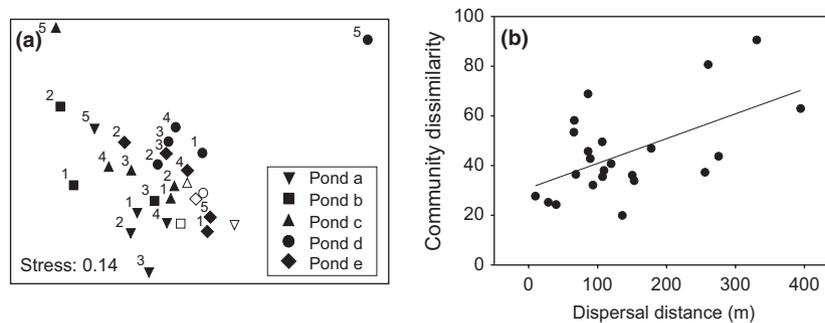

Fig. 3 (a) Multidimensional scaling (non-metric MDS) plot based on Bray Curtis dissimilarities illustrating differences in species composition hatched from sediment samples obtained from rubbing trees (filled symbols) and corresponding nearest source ponds (empty symbols), respectively. Samples from trees situated around different ponds are indicated by different symbols. Trees situated at increasing distances from source ponds are marked with numbers ranging from 1 to 5 (ranks). (b) Relationship between differences in community composition (Bray Curtis dissimilarity) and geographic distance between communities hatched from tree mud and communities hatched from the sediment of the corresponding nearest dispersal source.

heights of 150–300 cm, corresponding to the height of an adult elephant's flank.

Discussion

Detection of large numbers of invertebrate taxa as well as several plant diaspores embedded in sediment attached to rubbing trees at distances up to 400 m from the nearest potential source pond suggests that mammals are more important vectors for freshwater invertebrates than previously assumed (Peck, 1975; Allen, 2007; Vanschoenwinkel *et al.*, 2008c; Waterkeyn

et al., 2010a,b). Most sediment occurred at heights above 1.5 m, suggesting a dominant role for the African elephant, the only mud-wallowing mammal attaining this height. Elephants have already been reported to be prime dispersal agents of seeds of many trees, particularly in the primary rainforest (Cochrane, 2003; Kitamura *et al.*, 2007; Campos-Arceiz *et al.*, 2008) and semi-arid woodland habitats (Dudley, 1999, 2000). The current study has documented that elephants, and most likely other mud-wallowing mammals as well, may fulfil a similar role transporting aquatic invertebrates.
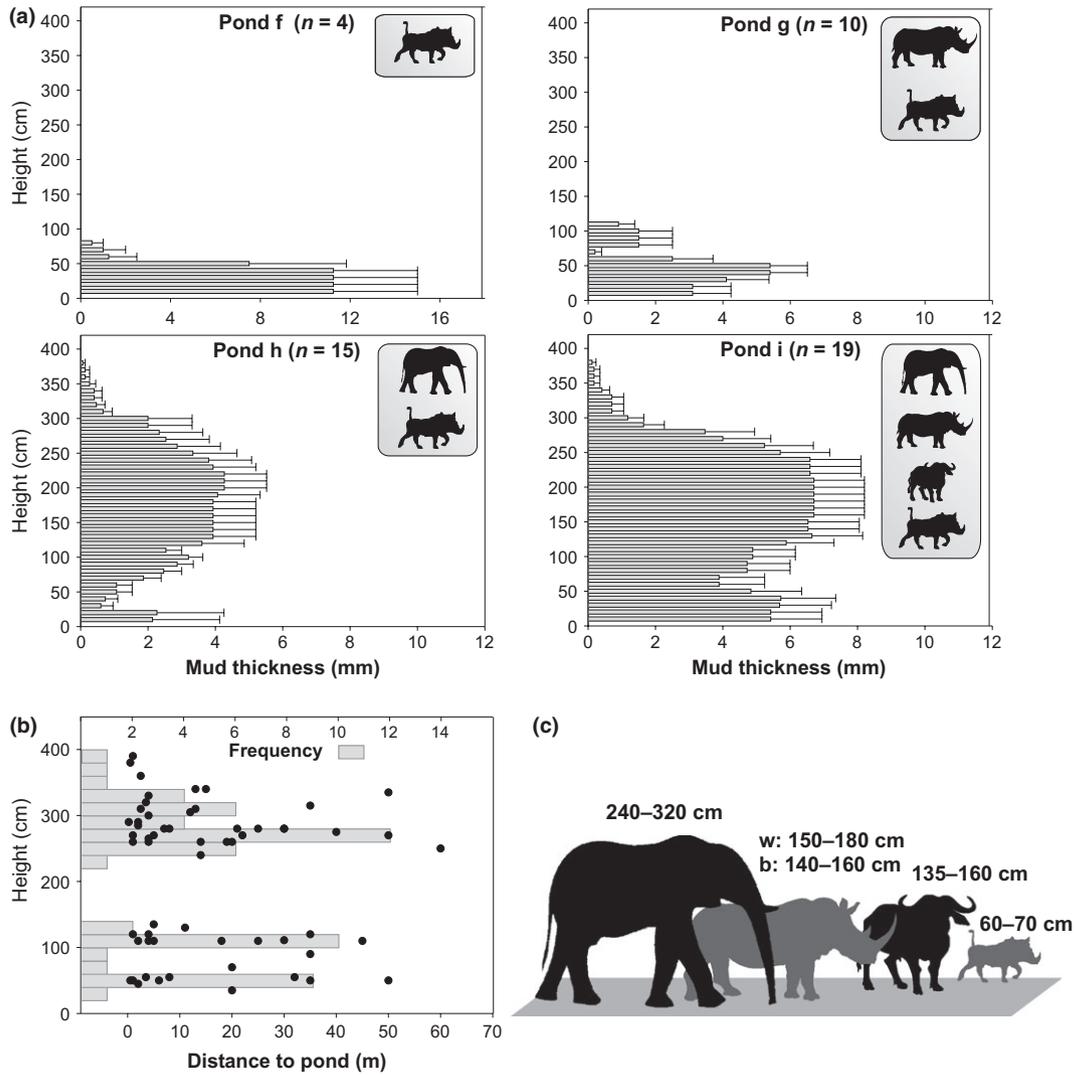
Fig. 4 (a) Relation between height and thickness (mean + SD) of mud depositions on rubbing trees situated near four ponds visited by different vector species. Confirmed vector species visits are indicated using corresponding silhouettes; *n*, number of rubbing trees located near each pond. (b) Frequency distribution of the maximum height of mud coverage on all rubbing trees mapped in this study. (c) Average shoulder heights of different candidate vector species (source: Estes, 1991, 1999) from left to right: elephant, rhinoceros, buffalo and warthog.

Distance decay of dispersal

Samples collected from trees at greater distances from source habitats contained less sediment, fewer propagules and a lower number of taxa than those closer to the source (Fig. 2). Passive dispersal rates typically decrease with distance from point sources (Bilton, Freeland & Okamura, 2001; Clobert *et al.*, 2001; Cousens, Dytham & Law, 2008) and both stochastic and deterministic processes can contribute to explaining this pattern as a result of propagules being distributed over wider areas (dilution effect) and intrinsic prop-

agule properties (dispersal limitation; Ozinga *et al.*, 2005). Similarly, lower richness of propagules at greater distance may be the result of a random numeric effect (rarefaction: Magurran, 2004) but can also reflect deterministic differences in dispersal ability. The facts that less sediment was retrieved on trees further away from potential sources and that common propagules are more likely to travel greater distances are consistent with a dilution effect and the importance of stochastic processes. Dispersing communities strongly reflected communities of the nearest dispersal source with similarities in species composition

between sample and source steadily decreasing with increasing dispersal distance (Fig. 3). At the spatial scale studied (0–400 m), no indications for differences in dispersal ability were detected although it is not unlikely that such differences may become evident at larger spatial scales. No indications were found for a potential importance of propagule size affecting dispersal ability, although this has been shown to be a limiting factor for passive dispersal in other systems and organisms (Salisbury, 1975; Meyer & Carlson, 2001; Vanschoenwinkel *et al.*, 2009; but see Brochet *et al.*, 2009, 2010a). This, perhaps, should not be surprising since attachment of mud is probably not a selective process and propagule properties may matter very little when these are embedded in a sticky matrix. In our savannah woodland, pond sediment predominantly consisted of thick sticky clay that easily attaches to vectors. In areas where pond sediment is more sandy, attachment success of propagules to vector animals can be expected to be much lower. As a result, as suggested by Figuerola & Green (2002), variation in sediment properties such as grain size, texture and moisture content could potentially affect ectozoochorous dispersal.

In general, taxa present in tree mud samples were also detected in sediment of the nearest potential source habitat. Exceptionally, a number of rotifer species as well as a limited number of germinating macrophytes were only found in tree mud samples and not in the propagule bank of presumed source ponds. It is possible that these propagules originated from other unsampled aquatic habitats in the area or that these taxa were missed during sampling of the ponds. The second possibility is particularly plausible for the macrophytes, which have patchy distributions in the ponds (B. Vanschoenwinkel, personal observation).

Feasibility of mammal-mediated dispersal

Nathan *et al.* (2008) identified three factors that contribute to the feasibility of different vectors: vector load (number of propagules transported), vector displacement (vector vagility) and passage time (duration of vector association). Although the maximum dispersal distance detected in this study was limited to 400 m from a nearest source, high vagility of mud-wallowing mammals suggests that their ability to disperse propagules will not be restricted to local scales. Many mud-wallowing mammals have

large home ranges, i.e. the area traversed during routine activities (African elephant: 50–3750 km², white rhino:. 5–90 km², black rhino: 2–500 km², buffalo: 126–1075 km², warthog 0.6–3 km²) and commonly migrate over long distances (African elephant: 12–20 km day⁻¹, white rhino: 20 km day⁻¹, black rhino: 8-25 km day⁻¹, buffalo: 5.5–40 km day⁻¹, warthog 7 km day⁻¹) (Douglas-Hamilton 1972; Hall-Martin, 1984; Owen-Smith, 1992; Prins, 1996; Estes, 1999). Particularly, elephants cover large distances with occasional long-distance migrations of more than 140 km (Owen-Smith, 1992) and, hence, are most likely to occasionally facilitate long-distance dispersal of aquatic invertebrates.

Currently, quantitative estimates of the amount of mud and the total amount of propagules attached to individual vector animals are unavailable, but the amount of mud commonly retained on an elephant's back can easily exceed 10 kg (B. Clegg, personal observation). Considering the high propagule densities observed in this study (± 1 propagule g⁻¹) vector load is likely to be very high. In waterbirds, where most propagules are transported internally (Brochet *et al.*, 2010a), empirical evidence suggests that vector loads are lower (0–1 propagules per dropping, Brochet *et al.*, 2010b: 20–50 propagules per dropping, Green *et al.*, 2008) although some studies reported higher propagule loads. A faecal sample from an Australian pelican, for instance, yielded 299 invertebrate resting eggs (Green *et al.*, 2008), while in Northern shoveler (*Anas clypeata*) up to 1000 propagules were retrieved from a single dropping (Figuerola, Green & Santamaria, 2003). In terms of dispersal potential, however, birds often will compensate for lower individual vector loads by being locally abundant and many species embark on long-distance seasonal migrations. The balance between birds and mammals in relative importance as vectors, however, may vary regionally. In Zimbabwe and southern Africa, for example, the density of waterbirds seems to be lower than in Europe (Gaston & Blackburn, 1996), and fewer of them are long-distance migrants (Delany & Scott, 2006). Thus, mammals may indeed be especially important for long-distance dispersal in this area.

Little is known about the duration of the association between propagules and vector animals. One could argue that rubbing behaviour will ensure that mud attached to the vector animal's skin will not be

retained for very long. Still, mud-wallowing mammals are regularly sighted covered with mud far away from potential sources (Owen-Smith, 1992). What is more, besides thermoregulation, disinfection of wounds, parasite control and a potential sexual function during the rut (Fernandes-Llario, 2005), mud may serve other functions such as protection from the sun that might stimulate animals such as elephants to retain a protective mud cover for prolonged periods of time. Additionally, nothing is known about gut passage time or the survival rates of propagules ingested by mammals. In wild boar, faecal samples were shown to contain a less diverse set of invertebrate propagules than those retrieved from mud depositions on rubbing trees (Vanschoenwinkel *et al.*, 2008c). This could suggest that, unlike for ducks (Brochet *et al.*, 2010a), ectozoochory is more frequent than endozoochory in mammals. Waterbirds tend to wash and preen in the water and cannot afford to carry too much mud because plumage must be kept in good condition for flight, waterproofing and thermoregulation.

Finally, it must be noted that in order for dispersal to be successful, transported propagules must be deposited in other aquatic habitats. Clearly, mud depositions on rubbing trees, although useful to test the feasibility and the scale of mammal-mediated dispersal, are not examples of effective dispersal, although rainfall and floods have been observed to wash off pond sediments deposited on trees (B. Vanschoenwinkel, personal observation) and may ensure that propagules eventually end up in aquatic habitats. Behavioural studies suggest that vector species regularly visit different aquatic habitats. Particularly in the rainy season, elephant and white and black rhinoceros wallow at least once a day and may visit different wallows during the same day (Owen-Smith, 1992). Additionally, besides habitats used for wallowing, vector animals also visit for drinking purposes ponds that are often not the same as those used for wallowing (B. Clegg, personal observation). Elephants only drink from clear, relatively clean water sources and, when water is readily available, may visit up to three different water holes to drink per day (Estes, 1991; Owen-Smith, 1992). Although no information is currently available about exact vector loads and attachment times, the frequency and intensity of dispersal on local scales (0–400 m) in combination with high vagility, the tendency to visit different

aquatic systems and the potential load of the vector species involved, make it likely that transport of mud frequently results in effective dispersal, including the possibility of long-distance dispersal.

Relative importance of different mammalian vector species

Spatial distributions of mud on trees provide some insights into the spatial scale of dispersal but also the frequency and identity of the vectors involved. Vertical distribution of mud on tree trunks in combination with tracks and hairs attached to tree trunks indicate that, besides elephants, warthog and rhinoceros are involved in dispersal. Quantitatively, buffalo are likely to be less important since these do not regularly wallow and such behaviour is usually restricted to bulls (Estes, 1991). In our study, indications for Cape buffalo as a vector in the form of hairs were discovered on just two trees situated around one pond (pond i). In contrast, elephants and white and black rhinoceros wallow on a daily basis when water is available (Owen-Smith, 1992) as do warthogs (Estes, 1999).

Variation in vertical distribution of mud on trees in combination with differences in vector vagility and vector load suggest that local differences in vector species composition may affect passive dispersal dynamics. In areas with large mud-wallowing mammals such as elephant, dispersal of aquatic organisms is likely to be much higher than in areas where they are absent. Similarly, gene flow and exchange of species may be more frequent among ponds that are more accessible or more attractive to large mammals.

Historical context

Presently, large- and medium-sized mammals are likely to be relatively marginal dispersal vectors of aquatic organisms in densely populated regions such as Western Europe and large parts of North America, where they are no longer abundant. This, however, does not mean this was the case in the past and there are exceptions. Some species, such as wild boar are still locally abundant and probably still fulfil an important role as dispersal vectors of aquatic organisms in habitats such as forest ponds and pools that are not frequently visited by waterbirds (Vanschoenwinkel *et al.*, 2008c). Additionally, since the Pleistocene,

large- and medium-sized mammals have all but disappeared from large parts of the planet as a result of increased interaction with humans and changing climate (Cardillo *et al.*, 2005). Until very recently, mud-wallowing mammals such as large bovines, but also elephants and rhinoceroses, were abundant in most terrestrial ecosystems, including those in Europe and the Americas (Owen-Smith, 1992). It is likely that mud-wallowing mammals once fulfilled a dispersing role for aquatic organisms in areas where they are no longer present or abundant. Currently, waterbirds and humans are probably the dominant dispersal vectors of freshwater organisms among the permanent ponds and lakes characteristic of urbanised landscapes such as Europe. Dispersal by large mammals, however, was probably far more important in Europe in the recent past, when livestock was moved around en masse along traditional corridors between seasonal grazing areas and markets ('transhumance', see Ruiz & Ruiz, 1986). What is more, before humans commenced drastic deforestation and large-scale agriculture, temporary ponds, forest pools, puddles and phytotelmata were probably the most common lentic water bodies in the landscape. This is still the case in old growth forests and rainforests. Since these are habitats that are rarely visited by birds, we dare to argue that mammal-mediated dispersal of freshwater organisms currently will be the most important in the remaining wilderness areas.

Acknowledgments

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