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Anemochory of diapausing stages of microinvertebrates in North American drylands

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Abstract

1. Dry, ephemeral, desert wetlands are major sources of windblown sediment, as well as repositories for diapausing stages (propagules) of aquatic invertebrates. Zooplankton propagules are of the same size range as sand and dust grains. They can be deflated and transported in windstorm events. This study provides evidence that dust storms aid in dispersal of microinvertebrate propagules via anemochory (aeolian transport).
2. We monitored 91 windstorms at six sites in the southwestern U.S.A. over a 17-year period. The primary study site was located in El Paso, Texas in the northern Chihuahuan Desert. Additional samples were collected from the Southern High Plains region. Dust carried by these events was collected and rehydrated to hatch viable propagules transported with it.
3. Using samples collected over a 6-year period, 21 m above the ground, which included 59 storm events, we tested the hypothesis that transport of propagules is correlated with storm intensity by monitoring meteorological conditions such as storm duration, wind direction, wind speed, and particulate matter (PM_{10}; fine dust concentration). An air quality monitoring site located adjacent to the dust samplers provided quantitative hourly measurements.
4. Rehydration results from all events showed that ciliates were found in 92% of the samples, rotifers in 81%, branchiopods in 29%, ostracods in 4%, nematodes in 13%, gastrotrichs in 16%, and tardigrades in 3%. Overall, four bdelloid and 11 monogonont rotifer species were identified from rehydrated windblown dust samples.
5. Principal component analysis indicated gastrotrichs, branchiopods, nematodes, tardigrades, and monogonont rotifer occurrence positively correlated with PM_{10} and dust event duration. Bdelloid rotifers were correlated with amount of sediment deposited. Non-metric multidimensional scaling showed a significant relationship between PM_{10} and occurrence of some taxa. Zero-inflated, general linear models with mixed-effects indicated significant relationships with bdelloid and nematode transport and PM_{10}.
6. Thus, windstorms with high PM_{10} concentration and long duration are more likely to transport microinvertebrate diapausing stages in drylands.

KEYWORDS
dispersal, invertebrates, temporary pools, wetlands, zooplankton

1 | INTRODUCTION

Temporary aquatic habitats in arid lands differ in their geomorphology and hydroperiod (Goudie, 2018). When seasonal monsoons sweep across these terrains, rain falls unevenly over the landscape, but eventually some basins are re-filled. Thus, microinvertebrates inhabiting these habitats are caught within a duality comprising short bouts of active life during wet episodes that are inevitably followed by long, intense dry periods. However, once re-filled active life quickly returns when diapausing (anhydrobiotic) propagules hatch, repopulate the habitat, and subsequently replenish the propagule bank. This cycle must be completed before evaporation leaves the basin dry, which may last for many years before the next refilling (Bogan, Boersma, & Lytle, 2013; Brendonck & De Meester, 2003; Hairston, Van Brunt, Kearns, & Engstrom, 1995; Rivas et al., 2018).

All organisms disperse during their life cycle (Tesson et al., 2015), either actively or passively. For aquatic microinvertebrates (e.g., protists, gastrotrichs, rotifers, cladocerans, copepods), dispersal of their propagules is passive, and occurs via the movement of animals (zoochory), flowing water (hydrochory), and/or the wind (anemochory) (Després et al., 2012; Figuerola & Green, 2002; Fontaneto, Ficetola, Ambrosini, & Ricci, 2006; Incagnone, Marrone, Barone, Robba, & Naselli-Flores, 2015; Ptatscheck, Gansfort, & Traunspurger, 2018; Rivas et al., 2018; Vanschoenwinkel, Gielen, Seaman, & Brendonck, 2008). Where active life is more or less continuous, passive dispersal is likely to be dominated by hydrochory and zoochory (Frisch & Threlkeld, 2005; Rogers, 2014; Van Leeuwen et al., 2013).

Winds blowing across arid lands entrain sediments in the form of dust (silts and clays < 50 μm) and sand (>50 μm) (Field et al., 2010), as well as the diapausing stages of microinvertebrates that when hydrated hatch into active communities (Rivas et al., 2018) (Figure 1). Important sources of aeolian (wind-carried) sediments emanating from arid lands include ephemeral wetlands (Bullard et al., 2011), such as playas (ephemeral lakes) (Mahowald, Bryant, Del Corral, & Steinberger, 2003) and intermittent streams (Draut & Rubin, 2008). Thus, along with mineral material, biota may also be entrained by winds. Studies examining the biological component of aeolian transport include viruses, algae, bacteria, fungi, lichens, bryophytes, plant and animal parts, and insect eggs (Amato et al., 2018; Delort & Amato, 2018; Després et al., 2012; Lönnell, Hylander, Jonsson, & Sundberg, 2012; Marshall, 1996; Ravi et al., 2011; Van Zanten, 1984). Although it has been demonstrated that biological materials with particle size ranges of between <1 and 100s μm are transported by the wind (Delort & Amato, 2018; Després et al., 2010), these studies did not specifically consider the resting stages of microinvertebrates.

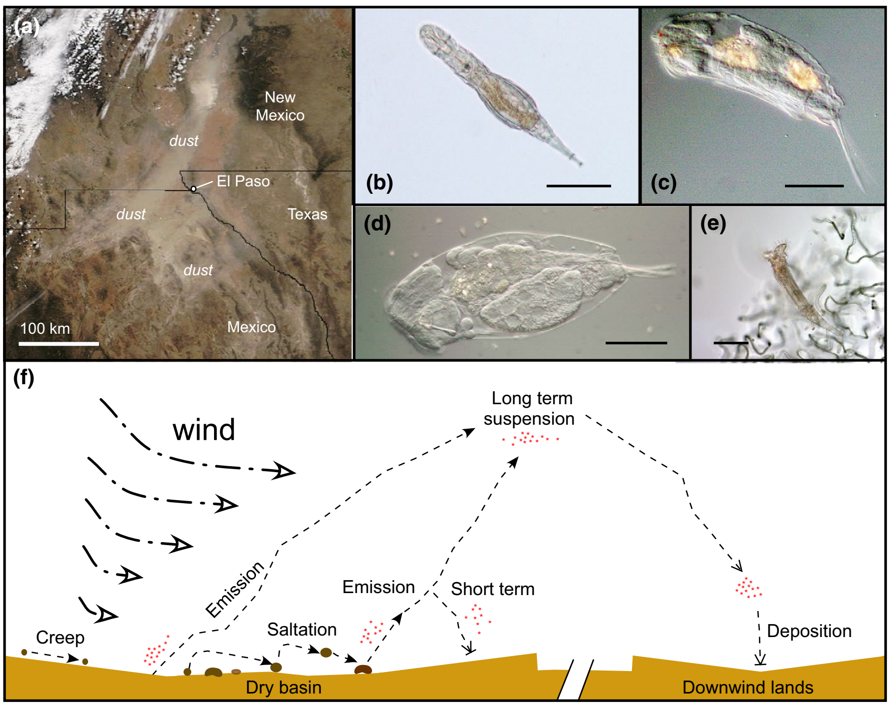

FIGURE 1 Dust emitted from dry wetlands travels long distances and is capable of transporting diapausing stages of aquatic microinvertebrates. (a) Satellite image of dust from dry playas, ephemeral rivers, and other sources that advect north-eastward from the Chihuahuan Desert of Mexico into New Mexico and Texas. NASA MODIS Aqua satellite image on 31 March 2017. https://earthobservatory.nasa.gov/NaturalHazards/view.php?xml:id=89960wileyonlinelibrary.com] (b–e) Photomicrograph of selected rotifers rehydrated from dust collections. (b) *Adineta vaga* (161 μm); (c) *Cephalodella tinca* (140 μm); (d) *Cephalodella* sp. (178 μm); (e) *Pleuretra lineata* (157 μm). Scale bars on b–e = 50 μm. Also see Rivas et al. (2018). (f) Synopsis of events leading to dust emission and deposition at desert surfaces. Red * = sandblasting also initiates the emission of dust particles (After Kok, Parteli, Michaels, & Bou Karam, 2012 and several other sources.) [Colour figure can be viewed at wileyonlinelibrary.com]

While earlier investigations have shown that propagules of aquatic protists may become aerosolised and thus may be transported downwind (Fenchel & Finlay, 2004; Finlay, 2002; Gislén, 1948; Hamilton & Lenton, 1998), the role of wind dispersal for zooplankton has not been clarified. For example, we do not know how propagule size, density, and shape influences dispersal distance (Tesson et al., 2015). While researchers have long posited that aquatic microinvertebrates can be transported by wind and there is ample indirect evidence for this (Table 1), few studies have actually monitored propagule movement during dispersal events (Tesson et al., 2015).

Using a multifaceted approach, Rivas et al. (2018) demonstrated that propagules of micrometazoans were transported up to regional distances by windstorms in the arid lands of southwestern North America and that many retained viability. Here, we expand that investigation to explore how transport of microinvertebrate propagules is correlated with physical properties of windstorms. To do this we collected airborne sediments and compiled physical and biological data from 59 major windstorm events over 8 years in El Paso, TX, U.S.A. Hereafter, we refer to wind-fallen sediment of all sizes as dust. The intensity of events was measured by duration of the windstorms, total amount of dust deposited, and particulate matter (PM_{10}) concentration (particles ≤10 μm in diameter) measured at an adjacent air quality monitoring station. To assess presence of diapausing propagules of aquatic microinvertebrates, we rehydrated subsamples in sterile, artificial hardwater and identified taxa that emerged over a period of several weeks. We used statistical methods to investigate potential relationships among taxa dispersed and features of the dust storms related to intensity. Thus, by monitoring meteorological conditions such as storm duration, wind direction, wind speed, and PM_{10} (fine dust concentration), we tested the hypothesis that transport of propagules is correlated with storm intensity. We also report findings of taxa found in airborne dust collected at four other wind-eroding localities in the Chihuahuan Desert and one in the adjacent Great Plains over a 17-year period.

2 | METHODS

The protocols described by Rivas et al. (2018) were followed, with the modifications noted below.

2.1 | Dust collection and characterisation

Collection sites in the Chihuahuan Desert included: (1) the Biology Building rooftop (BRT) at University of Texas at El Paso (UTEP), samplers were located *c.* 21 m above the ground level; (2) Hueco Tanks State Park and Historic Site, El Paso Co., Texas (HTSP), three samplers approximately 1 m above ground sites and one rooftop, approximately 3 m above ground; (3) White Sands Missile Range, New Mexico (WSMR), samplers that were *c.* 20 cm from the ground surface; (d) Jornada Experimental Range, New Mexico (LJER), samplers placed *c.* 2 m above the ground; (e) Salt Flat Basin, Texas (SB), samplers placed *c.* 0.5 or *c.* 1 m above the ground. The sixth site was located in the southern Great Plains (Yellow Lake, TX [YL]; samplers were *c.* 0.05, 0.1, 0.25, 0.5, or 1.0 m above ground; Figure 2). Sample collection was as described in Rivas et al. (2018). In brief, dust from windstorms (1999–2016) was collected using three standard types of passive collectors: Big Spring Number Eight (BSNE); Marble Dust Collector (MDCO); or Modified Wilson and Cooke (MWAC) (Goossens & Offer, 2000; Mendez, Funk, & Buschiazzo, 2011). Choice of the collector type was based on equipment availability and habitat conditions (Table 2).

The primary collection site was the BRT at UTEP where 59 of the 91 dust samples were collected. Nine MDCOs, with a total surface area of *c.* 0.9 m^2, were placed in different orientations on the rooftop the day before dust events were forecasted by the U.S. National Weather Service (NWS; El Paso forecast office, Santa Teresa, NM). Dust samples were collected on an event-by-event basis or long-term, which included multiple events. At HTSP, collectors were deployed for either an event-by-event basis or for the entire dust storm season (*c.* November–May in the Chihuahuan Desert). Dust collection from all sites involved removing deposited material that was then weighed and placed in a sterile container for additional analysis. For collections using MDCOs, marbles were rinsed and the rinsate was also monitored for emerging microinvertebrates (see 2.2 Rehydrations, below).

A record of the exact times of occurrence and meteorological characteristics of dust events in El Paso was obtained from the NWS. Airborne PM_{10} concentrations (including peak and mean hourly values during dust events) and meteorological data were obtained from the Texas Commission on Environmental Quality (TCEQ) monitoring station CAMS-12 located *c.* 200 m from the BRT site. Meteorological data were not available for events monitored at other sites. Wind direction was obtained from the NWS record of each dust event.

Biology Building rooftop dust collection events were classified according to peak hourly PM_{10} concentrations at CAMS-12. (a) Excluded events ($n = 7$) were those not included in statistical analyses because PM_{10} data were not available due to TCEQ sensor malfunction or data were not validated. (b) Low intensity and/or long-term (background) events ($n = 10$) included sample collections with $PM_{10} < 200$ μg/m^3 (range: 89–191 μg/m^3) and collection periods lasting weeks to months. (c) High intensity events ($n = 49$) in which PM_{10} was ≥200 μg/m^3 (range: 200–4,739 μg/m^3; Supporting Information, Table S1).

2.2 | Rehydration

In this study we rehydrated dust from an additional 75 events not previously reported in Rivas et al. (2018) comprising a total of 91 dust samples collected over 17 years. Dust samples were stored in individual sterile containers until processed for rehydration. To process the samples we used the following protocol. (a) Using a sterile spatula 1–2 g of dust was moved from its container to a sterile

TABLE 1 Selected studies of aquatic invertebrates transported on local, regional, and global scales via anemochory

Taxon	Scale of movement	Region	Reference
Rotifers			
Not specified	Local	S Shetland Islands	Janiec (1996)
Bdelloids	Local	Illinois, U.S.A.	Jenkins & Underwood (1998)
Monogononts, bdelloids	Local	Illinois, U.S.A.	Cáceres & Soluk (2002)
Not specified	Local	Antarctica	Nkem et al. (2006)
Monogononts, bdelloids	Local	Spain	Moreno et al. (2016)
Not specified	Local	Brazil	Lopes et al. (2016)
Monogononts, bdelloids	Regional	SW U.S.A.	Rivas et al. (2018)
Monogononts, bdelloids	Regional	SW U.S.A.	This study
Ciliates			
Colpoda steinii	Local	Mexico City	Rivera et al. (1992)
Not specified	Local	South Dakota, U.S.A.	Rogerson & Detwiler (1999)
Not specified	Regional	SW U.S.A.	Rivas et al. (2018)
Not specified	Regional	SW U.S.A.	This study
Not specified	Global	—	Finlay (2002)
Gastrotrichs			
Not specified	Regional	SW U.S.A.	Rivas et al. (2018)
Not specified	Regional	SW U.S.A.	This study
Branchiopods			
Branchipodopsis wolfi	Local	South Africa	Brendonck & Riddoch (1999)
Branchipodopsis wolfi	Local	South and Eastern Africa	Hulsmans, Moreau, De Meester, Riddoch, & Brendonck (2007)
Branchipodopsis tridens	Local	South Africa	Vanschoenwinkel et al. (2008)
Leptestheria striatoconcha	Local	South Africa	Vanschoenwinkel et al. (2008)
Branchinecta gaini	Local	Antarctica	Hawes (2009)
Artemia franciscana	Local	British Columbia, Canada	Parekh, Paetkau, & Gosselin (2014)
Various species	Local	Utah, U.S.A.	Graham & Wirth (2008)
Fairy, Clam, Tadpole shrimp	Regional	SW U.S.A.	Rivas et al. (2018)
Fairy, Clam, Tadpole shrimp	Regional	SW U.S.A.	This study
Tardigrades			
Isohypsibius asper	Local	S Shetland Islands	Janiec (1996)
Diphascon sp.	Local	S Shetland Islands	Janiec (1996)
Not specified	Local	Antarctica	Nkem et al. (2006)
Apodibius confusus	Local	Germany	Hohberg, Russell, and Elmer (2011)
Not specified	Regional	SW U.S.A.	Rivas et al. (2018)
Not specified	Regional	SW U.S.A.	This study
Nematodes			
Eudorylaimus and *Mesodorylaimus*	Local	S Shetland Islands	Janiec (1996)
Several genera listed	Local	California	Vigliercho & Schmitt (1981)
Several species	Local	South Africa	Baujard & Martiny (1994)
Scottnema lindsayae	Local	—	Nkem et al. (2006)
Several genera listed	Local	Germany	Ptatscheck et al. (2018)
Not specified	Regional	—	Carroll & Viglierchio (1981)
Not specified	Regional	SW U.S.A.	Rivas et al. (2018)
Not specified	Regional	SW U.S.A.	This study
Heterodera avenae	Global	—	Meagher (1977, 1982)

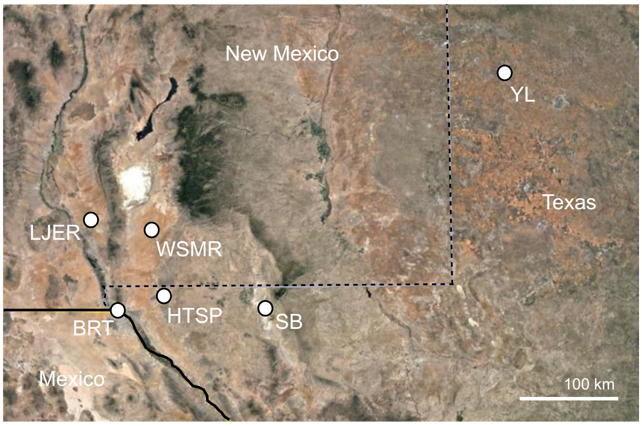

FIGURE 2 Map of collection sites used in this study. BRT = Biology rooftop, University of Texas at El Paso, El Paso Co., TX; HTSP = Hueco Tanks State Park and Historic Site, El Paso Co., TX; LJER = La Jornada Experimental Range, Doña Ana Co., NM; SB = Salt Basin, Hudspeth Co., TX; WSMR = White Sands Missile Range, Otero Co., NM; YL = Yellow Lake, Hockley Co., TX. State borders = dashed lines; solid lines = International borders. Google Earth Pro V 7.3.1.4507. Accessed 6/22/18 [Colour figure can be viewed at wileyonlinelibrary.com]

weigh boat and its mass determined. (b) To rehydrate the dust, it was then transferred to a 150 mm diameter, sterilised, glass Petri dish and 50 ml of sterile, modified MBL medium (Stemberger, 1981) was added. (c) Rehydrated samples were incubated at ambient room temperature and lighting conditions; the Petri dishes were kept closed at all times except when inspected for emerging invertebrates, which was done every 1–3 days for at least 1 month. (d) Emerging taxa were removed using a fresh, sterile pipette for each sample.

2.3 | Statistical analyses

For statistical analyses, rotifers were grouped into the broader categories of bdelloids and monogononts as other taxa were only identified to higher taxonomic levels (e.g., gastrotrichs). We separated the two types of rotifers because of fundamental differences in their diapausing stages (i.e., bdelloids, anhydrobiotic xerosomes versus monogononts, diapausing embryos).

2.3.1 | Amount of dust deposited and number of taxa transported

The relationship of taxa transported and dust deposition was first analysed using simple correlation analyses (Pearson's correlation) in GraphPad Prism 8.0.0 (GraphPad Software Inc., La Jolla, CA, U.S.A.).

2.3.2 | Storm characteristics and number taxa transported

Multivariate analyses, including principal component analysis implemented in CANOCO version 5.10 (Ter Braak & Smilauer, 2012), non-metric multidimensional scaling (NMDS) conducted in the *envfit* package, and zero-inflated Poisson (ZIP) binomial models with mixed-effects packages (R statistical software version 3.2.2) were done to determine how meteorological variables were associated with taxa found in the dust fallout for BRT samples only (n = 59). ZIP analysis was chosen because of multiple zeros in the taxonomic data set. Event features included: event intensity, mass of dust deposited, duration of the event, hourly peak and mean PM_{10} concentration, and wind direction (Supporting Information, Table S1).

3 | RESULTS

3.1 | Dust collection and characterisation

Sample collection from HTSP (n = 9), WSMR (n = 4), LJER (n = 4), SB (n = 1), and YL (n = 14) occurred non-consecutively over multiple years during the dry windy season. BRT samples (n = 59) were collected from all events during the entire 2011–2016 dust seasons. In 2010, samples were collected from selected events. Not all events provided valid data, however, due to rain or sampler malfunction of the dust traps or the TCEQ air monitoring station.

TABLE 2 Collection site information and summary of dust samples rehydrated. Sites included the Biology Building rooftop at the University of Texas at El Paso (BRT), Hueco Tanks State Park and Historic Site (HTSP), Yellow Lake (YL), and Salt Flat Basin (SB) all located in Texas; and White Sands Missile Range (WSMR), and La Jornada Experimental Range (LJER) both located in New Mexico. Collectors after Goossens and Offer (2000): BSNE, Big Spring Number Eight; MWAC, Modified Wilson and Cooke; MDCO, Marble Dust Collector. GPS coordinates and the number of events rehydrated from each site are also shown

Collection site	Collector type	GPS coordinates	Number of rehydrations from windstorm events
BRT (El Paso Co., TX)	MDCO	31.76873 N, 106.504067 W	59 (8)
HTSP (El Paso Co., TX)	MDCO/BSNE	31.926927 N, 106.041183 W	9 (3)
YL (Hockley Co., TX)	BSNE	33.823477 N, 102.459967 W	14 (2)
WSMR (Otero Co., NM)	MWAC	32.437503 N, 106.168744 W	4 (2)
SB (Hudspeth Co., TX)	BSNE	31.80 N, 104.97 W	1
LJER (Doña Ana Co., NM)	MWAC	32.608625 N, 106.730238 W	4 (1)

Note. Numbers in parenthesis indicate the number of samples rehydrated from each location that were previously reported in Rivas et al. (2018).

Sampler malfunction includes preventative maintenance and rejected or invalid data as indicated by TCEQ validators (Supporting Information, Table S1).

For dust samples collected at BRT, the mass of dust deposited per single high intensity dust event ranged from 0.56 to 18.2 g while low intensity, long-term (background) events yielded from 0.77 to 18.8 g. High intensity events had a peak hourly PM_{10} of 4,739 μg/m^3 compared to an hourly maximum of 166 μg/m^3 for low intensity events. Hourly average PM_{10} concentrations for full events ranged from 42 to 764 μg/m^3. Long-term dust collections at WSMR, LJER, and YL yielded a maximum of approximately 21 g, 5 g, and 39 g of material, respectively (Supporting Information, Table S1). The single sample collected from SB consisted of 2.5 g.

3.2 | Rehydration

Rehydration of collected dust yielded several species of bdelloid and monogonont rotifers (Figure 1b–e) along with algae, ciliates, gastrotrichs, ostracods, branchiopod nauplii, fairy shrimp, copepods, nematodes, and tardigrades. Rotifers were identified to genus or species, but were categorised as bdelloids or monogononts for statistical purposes. The number of taxa recovered ranged from 1 to 15. Rotifers accounted for *c*. 81% (*n* = 91 events) of taxa collected from all sites for each event. Additional rehydration results from all sites included ciliates found in 92% of samples, while branchiopods were recovered in 29%, ostracods 4%, nematodes 13%, gastrotrichs 16%, and tardigrades 3%. For BRT samples (*n* = 59), *c*. 80% of taxa were bdelloids and *c*. 10% were monogonont rotifers. *Collotheca* sp., *Ptygura beauchampi* Edmondson, 1940, and *Cephalodella sterea* (Gosse, 1887) were the monogonont species that emerged following rehydration. Bdelloids recovered included *Philodina tranquilla* Wulfert, 1942, *Adineta vaga* (Davis, 1873), and *Macrotrachela quadricornifera* Milne, 1886.

Of nine dust samples rehydrated from collections made at HTSP, *c*. 33% of the recovered taxa were bdelloids (e.g. *Philodina acuticornis* Murray, 1902, *Philodina* cf. *tranquilla*, *Pleuretra lineata* Donner, 1962). We found one monogonont species, *Lecane hornemanni* (Ehrenberg, 1834). Additionally, ciliates and nematodes were found in these samples. Only ciliates were recovered in the rehydrated samples from WSMR. From the four LJER samples rehydrated, two unidentified bdelloids and three monogonont rotifers (*Cephalodella catellina* (Müller, 1786); *Cephalodella tinca* Wulfert, 1937; *Cephalodella* sp.) were found. In the rehydrated LJER samples, we found ciliates, branchiopods, nematodes, and *Moina* sp. Rehydrations from SB dust samples yielded two monogonont rotifers (*Cephalodella* sp. and *Hexarthra* sp.); in one sample, ciliates and an ostracod also emerged. In the rehydrated YL dust samples, we found no bdelloids; however, 11 out of 14 samples contained monogonont rotifers including: *Rhinoglena ovigera* Segers & Walsh, 2017, *Cephalodella misgurnus* Wulfert, 1937, *Hexarthra fennica* (Levander, 1832), and *Proales similis* Beauchamp, 1907. Ciliates, gastrotrichs, ostracods, and branchiopods were also found.

3.3 | Statistical analyses

3.3.1 | Amount of dust deposited and number of taxa transported

When considering all sites and events, there was no correlation between the number of taxa transported and the mass of dust deposited (Pearson $r = 0.13$, $p = 0.23$). However, most taxa (up to 15) were recovered when deposition ranged from >1 g to 10 g. When deposition was <1 g, we found 1–2 taxa per event. One to eight taxa per event were recovered when the deposition was >10 g. The number of taxa present in rehydrated dust was also weakly correlated with the duration of the event (Pearson $r = 0.29$, $p = 0.02$). BRT events ranged from *c*. 1 to *c*. 15 hr. Events lasting only 1 hr yielded one taxon, yet some events lasting 2, 5, 7, or even 8 hr also produced only one taxon. Events of 8–10 hr typically transported five taxa, while the two events lasting 15 hr resulted in 2 and 14 taxa. There was a strong positive correlation between peak hourly PM_{10} concentration during events and taxa recovered from windstorm event samples (Pearson $r = 0.74$, $p = 0.0001$).

3.3.2 | Storm characteristics and number taxa transported

Using a multivariate principal component analysis approach, *c*. 83% of the total variation in distribution of taxa in relation to event characteristics was accounted for, with environmental variables explaining 38%. PC1 (*c*. 63%) showed a positive correlation of bdelloid rotifers with deposition. Monogonont rotifers, nematodes, and tardigrades were positively correlated with PM_{10} and duration. Branchiopods were positively correlated with duration, while gastrotrichs were correlated with compass degree (wind direction). PC2 (*c*. 19%) showed a positive correlation of gastrotrichs and compass degree (wind direction) and branchiopods with duration. Monogonont rotifers, nematodes, and tardigrades were positively correlated with PM_{10} (Figure 3a). Non-metric multidimensional scaling results show an association of gastrotrichs, bdelloids, monogononts, nematodes, and tardigrades with PM_{10} concentration ($r^2 = 0.25$; $p = 0.005$; Figure 3b; Supporting Information Table S2). A mixed model binomial ZIP distribution showed that the transport of bdelloids was significantly related to peak PM_{10} concentration ($z = 2.71$: $p = 0.007$) during dust storms. Nematode transport was also significantly correlated to peak PM_{10} concentration ($z = 2.35$; $p = 0.019$). There was no significant relationship between branchiopod transport and any of the environmental variables. Similarly, gastrotrich transport was not significantly related to any environmental variable; however, there was a weak association with PM_{10} and compass degree (wind direction; $z = 1.69$, $p = 0.091$; $z = 1.79$, $p = 0.074$, respectively).

4 | DISCUSSION

Effective anemochory of desiccated propagules requires that they remain viable during the entire process, including entrainment by

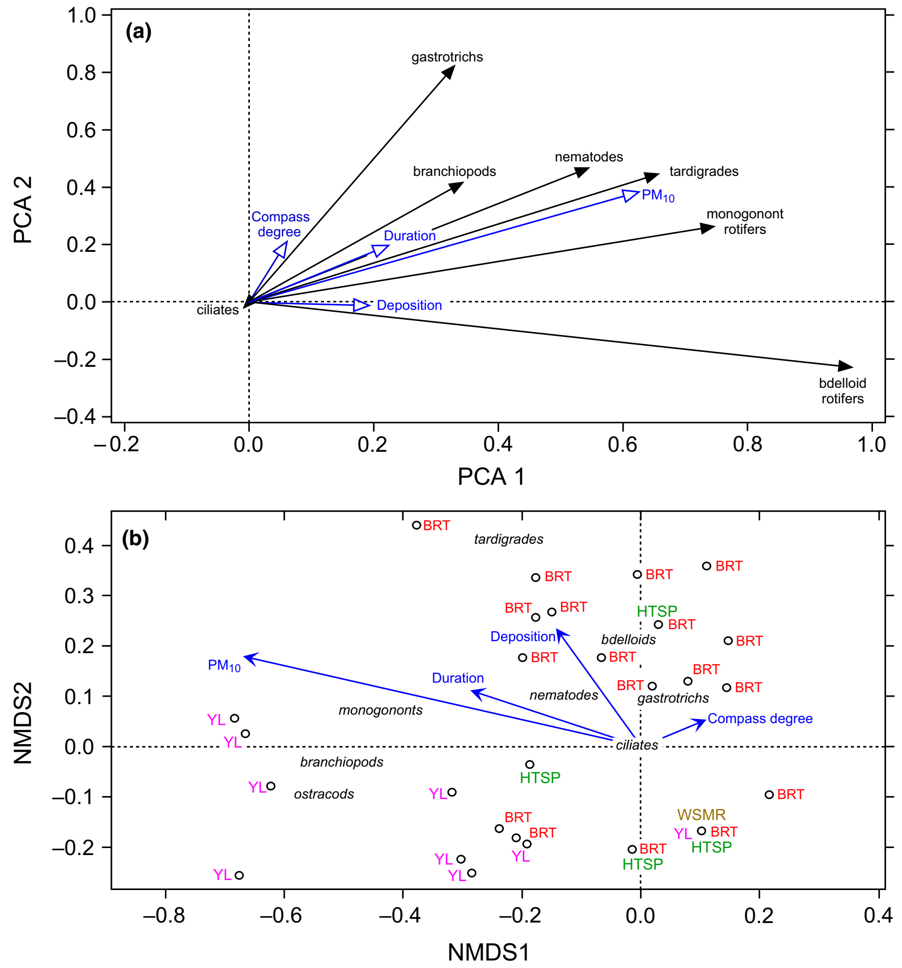

FIGURE 3 Meteorological variables and taxa found in dust from samples collected at the Biology Building rooftop (BRT) at the University of Texas at El Paso, El Paso Co., TX, U.S.A. (a) Principal component analysis (PCA) biplot. (b) Non-metric multidimensional scaling (NMDS). Abbreviations are defined in Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

winds, dispersal to a different habitat (Figure 1f), and hatching. While the literature is replete with examples of this phenomenon across a wide array of taxa, we recognise that artificial rehydration protocols, including ours, may not be suitable to initiate hatching of all viable propagules (May, 1987; Rivas et al., 2018; Vandekerkhove et al., 2005). Propagules may have a range of hatching conditions and bet-hedging strategies have often been invoked to explain differential hatching patterns from lake sediments (García-Roger, Serra, & Carmona, 2014; Walsh, Smith, & Wallace, 2014). Nevertheless, our study yielded a large number of taxa, including 91 events in which rotifers were present. Thus, we may assume that these results represent a minimum number of taxa and that others may have hatched had we used a more intensive rehydration protocol.

Many studies have shown that bacteria can be transported vast distances by wind (Wilkinson, Koumoutsaris, Mitchell, & Bey, 2012; reviewed in Després et al., 2012). Gislén (1948) provides an early discussion of microbial transport. This is probably due to the unique properties of bacterial endospores including their small size and resistance to ultraviolet radiation (UVR). For example, Creamean et al. (2013) showed that biological aerosols could be transported from as far as the Sahara and Asia to the western U.S.A., and Smith et al. (2013) detected microbial biomass in transpacific air plumes. Hamilton & Lenton (1998) demonstrated one mechanism whereby marine bacteria may be aerosolised by bubble-burst processes in wave-cap formation.

Although much larger, the propagules of aquatic microinvertebrates are still small enough to be entrained along with dust, and many are resistant to desiccation. Thus, they ought to be readily dispersed. However, the question of whether their capacity to disperse results in distributions characterised as cosmopolitan or localised remains unresolved. Rotifers provide a good example of this problem. Rousselet (1909) posited that rotifers have a cosmopolitan distribution and that localised distributions were accounted for by the fact that no country had been thoroughly surveyed. However, while Rousselet's comment on exploration remains valid, other assessments argue that dispersal followed by vicariance may explain endemicity in some regions (e.g. Australia), but that cosmopolitanism prevails in others (e.g. Africa and India) (Dumont, 1983).

In a recent review of rotifers of temporary waters, Walsh et al. (2014) noted that rotifers in ephemeral wetlands are likely to have a high dispersal capacity. This assessment was supported by the work of Rivas et al. (2018) that demonstrated propagules of zooplankton, especially those collected from desert dust samples, fall within the same size range as the mineral grains of dust and sand blown regionally in wind events. Additionally, the authors presented a detailed conceptual model showing the process of dispersal of zooplankton propagules. This model illustrates how wind events aid in the transport of these resting stages thereby showing potential for colonisation on a regional scale.

Here we expanded our previous results—that windstorms can transport aquatic microinvertebrate propagules across regional scales in the drylands of the southwest U.S.A. (Rivas et al., 2018)—by analysing a total of 91 wind events spanning 17 years. In doing so we (a) provided a more comprehensive investigation of which taxa are capable of being dispersed and (b) tested the hypothesis that transport of diapausing stages is correlated with the characteristics of dust storms in which they were entrained. We used statistical analyses to show that PM_{10} concentration has a significant role in determining which taxa are transported during dust storms. Duration of these events and, for some taxa, wind direction are also important. These factors are used to characterise dust storm intensity, especially PM_{10} concentration (Krasnov, Katra, Koutrakis, & Friger, 2014). Thus, our hypothesis that transport of viable propagules of microinvertebrate is dependent on storm intensity was supported.

Past studies have demonstrated that meteorological events, such as wind, play active roles in dispersal of microinvertebrate propagules (Cáceres & Soluk, 2002; Després et al., 2012; Havel & Shurin, 2004), particularly for ephemeral systems (Brendonck, Pinceel, & Ortells, 2017). For example, Tronstad, Tronstad, and Benke (2007) collected windfallen, dry-deposited microcrustaceans, including Cladocera, Copepoda, and Ostracoda from collection trays deployed at ground level within a temporary aquatic floodplain in a humid, non-dusty subtropical environment. However, these studies were based on local transport with sampling collectors placed within close proximity to water sources and/or near to the ground (Janiec, 1996; Jenkins & Underwood, 1998; Lopes, Bozelli, Bini, Santangelo, & Declerck, 2016; Moreno, Pérez-Martínez, & Conde-Porcuna, 2016; Nkem et al., 2006). Experiments presented in this study and Rivas et al. (2018) were novel compared to prior investigations as we demonstrated consistent transport of propagules within dusty windstorms in an arid environment. For example, the nearest water source in this study was *c*. 850 m from the collectors that were positioned 21 m above the ground. This height is consistent with potential dispersion of suspended material tens to hundreds of kilometres from a dust source (Rivas et al., 2018).

As previously noted, Rivas et al. (2018) performed particle size analysis on dust collected during windstorm events. The size ranges of dust particles overlapped with the size ranges of zooplankton propagules. For example, the diapausing embryos of monogonont rotifer range in size from *c*. 50 to 265 μm (Gilbert, 1974; Walsh, May, & Wallace, 2017) and bdelloid xerosomes are up to *c*. 120 μm (Ricci, Caprioli, Fontaneto, & Melone, 2008). Dust landing at the BRT site was previously inferred to originate from ephemeral wetlands up to hundreds of kilometres upwind from meteorological modelling and interpretation of satellite imagery based on airflow back-trajectories using HYSPLIT (Rivas et al., 2018). Winds for most events crossed ephemeral wetlands to the southwest on their path towards the BRT site. This includes the Paleo Lake Palomas Basin and other playas in northern Chihuahua (Baddock, Gill, Bullard, Dominguez Acosta, & Rivera Rivera, 2011; Baddock, Ginoux, Bullard, & Gill, 2016; Rivera Rivera, Gill, Bleiweiss, & Hand, 2010). Other likely source areas included White Sands, New Mexico (White et al., 2015), dry river beds, alluvial flats, and agricultural lands (Baddock et al., 2011; Rivera Rivera et al., 2010), and long stretches of episodically-wetted, dust-producing desert and urban soil surfaces (Baddock et al., 2011; García et al., 2004; Rivas et al., 2018). The nearest ephemeral wetland to the BRT sampling site is the floodplain of the Rio Grande, located *c*. 850 m upwind. However, microinvertebrate species previously identified from this floodplain (Walsh, unpublished data) were not recovered in dust at the BRT site.

An extreme drought occurred beginning in late 2010 across the south-western U.S.A. including the Chihuahuan Desert, and continued through 2014 (Heim, 2017; Nielsen-Gammon, 2012). As a result, an increasing area of wetlands became desiccated, and sediment from playas and other ephemeral wetlands were more prone to wind erosion and likely to be easily lofted into the atmosphere during high wind events during this period (Ponette-González et al., 2018).

We found variation between the number of taxa rehydrated and the duration of the wind event. Some events lasting only a few hours yielded few to many taxa, yet other events lasting several hours also yielded the same range of microinvertebrate diversity. This may be due to varying PM_{10} concentrations, as well as the species richness of ephemeral wetlands emitting dust during each event. For example, a case of PM_{10} of 1,387 μg/m^3 yielded one taxon, yet an event with a PM_{10} concentration of 4,739 μg/m^3 had 14 taxa. Another event with a PM_{10} of 250 μg/m^3 yielded four taxa. In these cases, wind direction was within the same general trajectory indicating similar dust sources, but because dust emissions from ephemeral wetlands are controlled by highly localised, microscale variations in wind gusts (Engelstaedter & Washington, 2007; Lee, Gill, Mulligan, Dominguez Acosta, & Perez, 2009), the exact points from where dust will be emitted will be different in every wind storm.

In this study, the number of taxa transported had a strong association with PM_{10} concentration. As noted above, PM_{10} concentrations are an indicator of the intensity of dust storms (Krasnov et al., 2014). Previous studies investigating fungal, microbial, and pollen transport with dust showed that there was a correlation of biota loading in the atmosphere with high PM_{10} concentrations (Sousa et al., 2008); Alghamdi et al., 2014). Further, Alghamdi et al. (2014) asserted that the transport of fungal species differed between events with differing $PM_{2.5}$ and PM_{10} concentrations. Additionally, Meklin et al. (2002) asserted that biological aerosols tend to attach to coarser PM fractions, and Ricci, Melone, Santo, and Caprioli (2003) stated that desiccating bdelloids tend to attach tightly to sediment grains. The findings of prior studies (Alghamdi et al., 2014; Sousa et al., 2008) also support our results in which taxa transported in wind events were positively correlated with PM_{10} concentration, and to lesser extent, related to the amount of sediment deposited.

We confirmed the viability of propagules that may have been transported up to hundreds of kilometres in very dry desert air.

Viability of propagules is probably related to factors such as lipid content and cyst wall composition (Boschetti, Pouchkina-Stantcheva, Hoffmann, & Tunnacliffe, 2011; Denekamp, Reinhardt, Kube, & Lubzens, 2010). Lipid content may be important by serving as storage products in propagules, which support low metabolism and facilitate prolonged diapause (García-Roger & Ortells, 2018). Tough walls also may allow diapausing stages to resist harsh environments, especially turbulent collisions with sharp, glasslike dust and sand particles during wind emission and transport. To simulate emission of propagules during windstorms, Rivas et al. (2018) tested entrainment and viability of propagules of seven taxa using a wind tunnel. They found that propagules of *Brachionus calyciflorus* Pallas, 1766, *Brachionus plicatilis* Müller, 1786, and other aquatic taxa were successfully transported and remained viable after recovery from all sections of the wind tunnel which simulated transport of up to *c*. 100 km.

In addition, physical properties of propagules (e.g. mass and morphology) are known to influence deflation and transport. For example, Graham and Wirth (2008) reported that large branchiopod cysts are capable of being moved over arid lands at wind velocities as low as *c*. 6 m/s. Pinceel, Brendonck, and Vanschoenwinkel (2016) showed that propagule morphology was important to their entrainment and subsequent dispersal in a small-scale laboratory experiment. Compared to the particles in playa sediments, a propagule probably has a much lower mass to volume ratio, and probably a more aerodynamic shape (Jenkins et al., 2007). This may allow easier entrainment and transport by the wind than a smaller sized mineral grain.

Bdelloid rotifers were found more frequently than monogononts in our dust samples. This may be due to their adherence to sediment grains and plant fibres (Ricci et al., 2003), thus facilitating transport of xerosome during wind events. In monogonont rotifers, the nature of the resting egg structure provides some protection from exposure to UVR and harsh chemicals (Radzikowski, 2013), and the dark colour of rotifer diapausing stages can further facilitate their resistance to the harmful effects of solar radiation to which they would be exposed during anemochory. In addition, thick concentrations of dust particles provide shielding from and scattering of UVR during long-distance transport, increasing survivability of biota transported within desert dust clouds (El-Askary, LaHaye, Linstead, Sprigg, & Yacoub, 2017; Prospero, Blades, Mathison, & Naidu, 1999). However, airborne clouds of dust and sand, especially when they originate from contaminated soils or pass through urban or industrial areas, will also contain gaseous and particulate pollutants that are known to be toxic to adult rotifers (Verma et al., 2013). A remaining question is whether the interaction of airborne resting stages with pollutants affects their viability during anemochory.

Thus, our research challenges previous studies that suggest that microinvertebrates do not readily disperse by anemochory (e.g. Jenkins & Underwood, 1998; Segers & De Smet, 2008). Therefore, our findings reinforce the call for increased collaboration among population biologists, atmospheric physicists, landscape ecologists, and modelers to create a holistic view of how anemochory affects development of zooplankton communities (Tesson et al., 2015). Nevertheless, additional research is needed to fill several gaps in our knowledge. For example, the relative contribution of propagules from dried wetlands as compared to periodically wet soils and cryptogamic crusts warrants study. Additionally, the influence that humans have on aeolian transport from all sources also needs to be investigated more thoroughly (Neff et al., 2008; Wilkinson, 2010). Another gap in our knowledge is the importance of prioritisation effects in establishing aquatic communities. De Meester, Gómez, Okamura, and Schwenk (2002) conceptualised this idea in their Monopolization Hypothesis, which posits that dispersal does not always result in successful colonisation. To explore these effects, we suggest using a mesocosm approach parallel to those used to explore metacommunity dynamics (e.g. Downing & Leibold, 2010), where established communities are seeded with propagules, in this case, those collected from fallen dust. Also, collections of dust samples at various elevations above ground should be conducted to determine whether taxa are transported at different heights during windstorms. Such efforts will provide information showing the potential for aquatic microinvertebrates to be transported differentially across local, regional, and global scales.

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CONFLICT OF INTEREST STATEMENT

None of the authors of the manuscript have any conflict of interests to report.

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