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# Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities

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Despite an upsurge of interest in spatial interactions between communities and in the impact of dispersal on ecological and evolutionary processes, dispersal patterns and dynamics in natural metacommunities remain poorly understood. Although passive aerial dispersal of freshwater invertebrates is generally accepted, the frequency and relative importance of wind as a vector is still subject of considerable debate. We assessed the importance of wind dispersal in an invertebrate metacommunity in a cluster of 36 temporary rock pools on an isolated mountaintop in South Africa. Wind dispersal was quantified every four days using nine windsocks (about 1.5 m above rock base), placed in the field during one month. Distance to the nearest pool varied from 2 up to 16 m. Wind direction and speed were monitored for the entire period. About 850 propagules (mostly resting eggs) of 17 taxa were captured. The presence of water in the pools (level of exposure of the dormant propagule bank) and the dominant wind direction were the key factors affecting the yield. Wind speed was much less important.

Our results suggest that wind dispersal of propagules from temporary aquatic systems is more frequent than previously thought. This may stabilise the metacommunity by mediating gene flow among populations and facilitating rapid (re)colonisation of patches. On the other hand, wind erosion of the dormant propagule bank may lead to egg bank depletion and local extinction.

The measured frequent wind dispersal most likely fuels strong species sorting processes ultimately shaping the structure of the local communities as observed in an earlier study. To elucidate the link between local dispersal rates and their contribution to long range dispersal is a major challenge for future research on aerial dispersal of aquatic invertebrates.

Different researchers have raised interest in the passive overland dispersal of small aquatic organisms ever since Darwin (1859) pointed at the quasi cosmopolitan distributions of many protozoan and zooplankton species. Traditionally, animals, water connections and wind are recognised as dispersal vectors (Bilton et al. 2001). Maguire (1963) suggested that the link between distribution and dispersal ability can be studied either by observing the colonization of isolated water bodies or by capturing organisms during transport. A third way is to infer dispersal rates indirectly from patterns of genetic differentiation (Neigel 1997, Bossart and Prowell 1998). However as dispersal and gene flow are not synonymous due to local interactions determining establishment success (De Meester et al. 2002), such indirect estimates are often not sufficient to describe and understand dispersal patterns (Bossart and Prowell 1998).

Louette and De Meester (2005) have shown that some zooplankton species are able to colonise new water bodies very quickly, relying solely on passive dispersal. The general importance of passive dispersal in zooplankton, the relative importance of different dispersal vectors and the efficiency of subsequent colonization, however, is still subject of considerable debate. Zooplankton are known to disperse readily between aquatic systems that have either permanent (Cladocera; Michels et al. 2001) or temporary connections (large branchiopods; Hulsmans et al. 2006). Additionally a large amount of evidence has accumulated confirming the importance of mostly waterbirds (Figuerola and Green 2002, Green and Figuerola 2005) but also amphibians (Bohonak and Whiteman 1999), reptiles (Lopez et al. 1999) and crayfish (Moore and Faust 1972) as animal vectors. Wind is probably the least studied dispersal vector. Experimental studies which excluded animal vectors subscribe the importance of wind as a main vector mediating stochastic dispersal events (Cáceres and Soluk 2002, Cohen and Shurin 2003). Relatively few researchers have tried to measure wind dispersal in a straightforward way by intercepting dispersing propagules. Brendonck and Riddoch (1999) measured only limited short distance dispersal ($<1$ m) in Anostraca of temporary rock pools in Botswana during a three day period, using sticky surfaces mounted around the pools. Jenkins and Underwood (1998), during a one year study, only intercepted rotifer propagules using two windsocks to study aerial dispersal of zooplankton from permanent ponds at distances of respectively 150 and 400 m from the wind socks.

Many invertebrates survive recurrent unfavourable periods as dormant life stages (Hairston 1996, Brendonck and De Meester 2003, Cáceres and Tessier 2003). In many species these resistant propagules also facilitate overland dispersal (Panov et al. 2004). In temporary aquatic systems, the dormant propagule bank is, at least for some time of the year, directly exposed to wind action, whereas it generally remains submerged in permanent waters. We therefore expect that wind dispersal of organisms from this type of habitat may be more important than from permanent waters.

Vanschoenwinkel et al. (2007) demonstrated, in a cluster of temporary rock pools situated on an isolated mountain top in South Africa, that pools with similar environments hosted similar communities and suggested that dispersal was probably not limiting. As the study site is characterized by strong winds during the season when most pools are dry, the authors hypothesized that wind dispersal could explain this effectiveness of species sorting processes.

In this study we explicitly tested the hypothesis of frequent wind dispersal in this metacommunity using nine wind socks, strategically positioned on the outcrop. Yields were collected once every four days during a one month period at the end of the rainy season. First we described the dispersing community and quantified the frequency of dispersal for the different taxa. Second, we tried to uncover any temporal and spatial patterns in the structure and richness of the dispersing community and to explain these patterns by relevant environmental variables such as wind speed, wind direction, isolation and the exposure of the dormant propagule bank.

## Study site

The study site (Fig. 1) consists of a cluster of rock pools including 36 basins (area: 0.6–50 $m^2$) and a larger number of small depressions and cracks. Pools are located on a flat sandstone rock ledge at the summit of the Korannaberg mountain, situated in the eastern part of the Free State Province (South Africa). Rainfall in the area is mostly restricted to the summer period (October-February). Low precipitation and high evaporation rates causes pools to be of a temporary nature.

### Material and methods

The study took place from 24 July until 24 August 2006. Windsocks consisted of a conical sock (100 μm mesh) with a maximum diameter of 30 cm and a total length of 90 cm attached to a stainless steel frame (Fig. 2). The tip of the windsock was curved and a zipper was integrated 30 cm from the tip to facilitate the removal of the collected samples. The metal frame consisted of two stainless steel rings of 30 and 20 cm in diameter respectively, connected by four 30 cm long crossbars. This rigid structure ensured a fixed opening of the mouth of the wind sock, even under conditions of low wind speed. The windsock was able to rotate freely around a stainless steel axis. Even under conditions of low wind speeds the mouth of the wind sock was always directed towards the current wind direction. The whole structure was anchored in a plastic parasol stand filled with ca 15 kg of sand. Stones were applied on top of the stand to provide extra stability.

A total of nine windsocks were placed in the field. Six were positioned more or less along a linear transect (NW-SE) along the rock ledge to cover a gradient of isolation. Two additional wind socks were placed left and one right of the central pool cluster (Fig. 1), to include variance in orientation towards the central pool cluster in our analysis. Distance to the nearest pool varied from two up to 16 m. Wind socks were emptied once every four days during one month (24 July until 24 August 2006), each day at 11 a.m. The one exception was the last collection, which was taken three days after the previous one, in order to prevent destruction of the equipment by a forecasted severe storm. Sample dates were t1: 24 July, t2: 28 July, t3: 1 August, t4: 5 August, t5: 9 August, t6: 13 August, t7: 17 August, t8: 21 August and t9: 24 August. During collection, windsocks

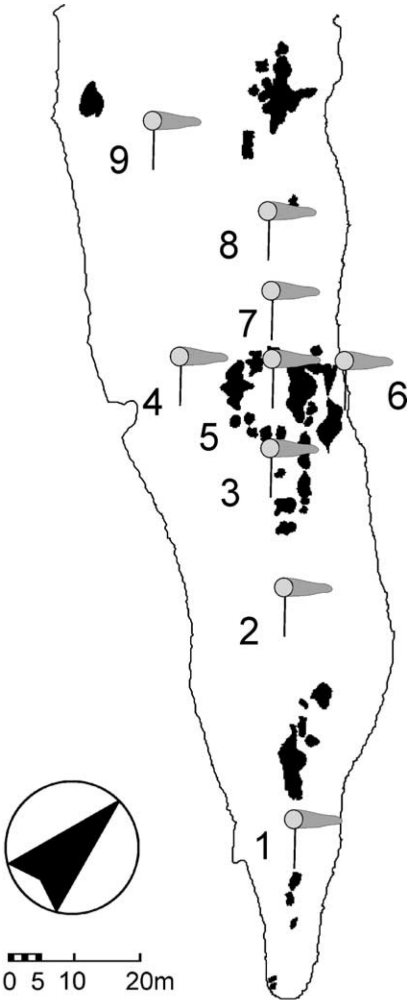

Fig. 1. Set up of the nine wind socks on the study site. Black patches represent rock pools.

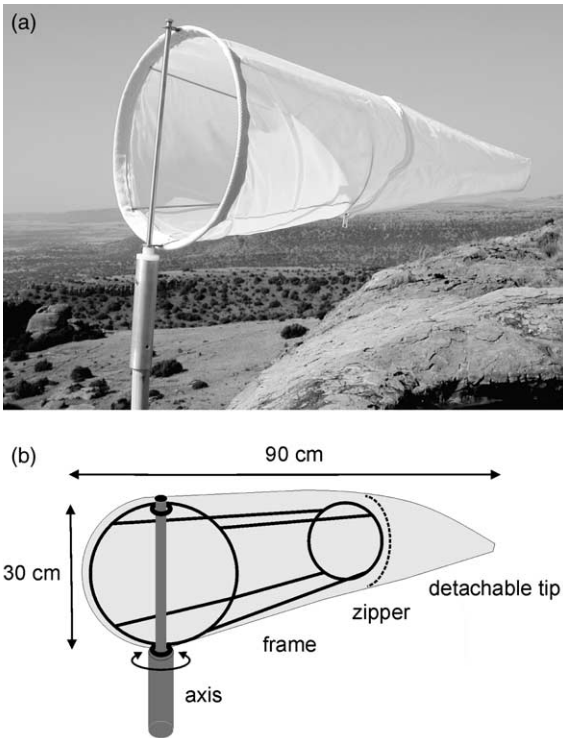

Fig. 2. (a) Picture of an experimental windsock in the field; (b) detailed schematic drawing illustrating the design of the experimental wind socks. Essential parts such as the zipper to detach the tip of the sock and the metal frame used to keep the mouth of the wind sock open at all times are indicated.

were thoroughly rinsed with 70% ethanol. The tip of the bag was unzipped and the contents transferred in a sample vial with 70% ethanol. Propagule communities (eggs, cysts, ephippia, juvenile and adult life stages) were analysed in the laboratory using a stereo microscope. Smaller resting eggs were studied in more detail under a higher resolution microscope. Organisms smaller than 100 μm such as rotifers and Protozoa were not included in this study as the 100 μm mesh size did not allow reliable collection of smaller sized propagules.

All animal dormant propagules were counted and identified using literature where available (Cladocera: Flößner 2000, Vandekerckhove et al. 2004, Oribatidae: Engelbrecht 1975, Turbellaria: De Roeck pers. com.). To be able to assign unknown propagule types to specific taxa, a mixture of pool sediment from 15 different rock pools was incubated in the laboratory in EPA medium (Anonymous 1985, 20 μS cm$^{-1}$, 20°C). Hatched species were isolated and cultivated up to egg deposition/propagule production to allow morphological comparison of produced propagule types with unknown propagules from the wind samples. Eggs of Anostraca and Spinicaudata as well as ephippia of Cladocera were identified to species level. Three types of chydorid ephippia could not be attributed to known species, and were referred to as belonging to the informal taxa chydorid B, D and E. We distinguished two ostracod taxa: *Heterocypris* sp. and *Korannacythere devriesi*. Copepods were attributed to the orders Harpacticoida or Calanoida. Bryozoan statoblasts, Turbellaria resting eggs and cryptobiotic Nematoda could not be identified to a lower taxonomic level.

We only included propagules or individuals in our analysis that were deemed viable. Anostraca and Spinicaudata eggs were considered viable when a well defined embryo popped out when squeezed (for method see Brendonck and Riddoch 2000b); Cladoceran ephippia when they contained intact eggs without external signs of degradation; Oribatidae, Ostracoda and cryptobiotic Harpacticoida when their appendages were intact. For some taxa e.g. bryozoan statoblasts, viability could not be verified from external structure.

An unexpected thunderstorm on 4 August inundated all pools. This created the opportunity to study the effect of level of exposure of the dormant propagule bank on wind dispersal. After eight days of inundation (little exposure to wind), water was pumped out from a number of pools to allow another dry spell (more wind exposure). On 12 August (just before t6) the water level of five pools (pools: 8, 9, 15, 24 and 29) was reduced to about 1.5 cm above the dormant propagule bank using a generator powered pump. On 13 August the same was done for another seven pools (3, 4, 22, 23, 31, 32, 34). Care was taken that the dormant propagule bank was not disturbed in this process. All removed water was filtered over 64 μm gauze and the sediment containing invertebrate propagules was carefully returned to the pool. All equipment was thoroughly rinsed before moving to another pool.

## Statistical analyses

### *Environmental variables*

Anemometer data were collected by the South African weather service at the weather station of Ficksburg (60 km east of the study site) and included average and maximal wind speed (m s$^{-1}$), wind direction (degrees), % calms (the percentage time with zero wind speed). Wind variables were averaged over each sampling interval using Wind analysis software by West (2005).

At the beginning of each time interval the ‘number of dry pools’ was added up and used as a predictor variable. Analogously, the cumulative surface area of exposed propagule bank (‘reb area’) was calculated by adding up the surface area of propagule bank of all the pools that were dry at the beginning of each time interval. The pool specific surface area of exposed propagule bank was drawn to scale and quantified using a digital planimeter At the beginning of the study period most pools were dry (28 out of 36). By t3, 31 pools were dry and a total of 160 m$^2$ of propagule bank was exposed. Heavy rains just before t4 covered the propagule bank of all 36 pools. The combined effect of evaporation and pumping resulted at t8 in 18 dry pools and 126 m$^2$ of exposed propagule bank.

The dominant wind direction during the entire study period was calculated using wind analysis software by West (2005). As wind direction limits the number of source pools for dispersing propagules for each windsock, the number of pools that were situated upwind as well as the upwind exposed area of dormant propagule bank, were integrated as variables: ‘no. pools upwind’ and ‘area reb upwind’. Isolation was estimated for each windsock using two parameters: the distance to the edge of the nearest pool (‘near pool’) and the average distance to another pool ('isolation') (the sum of the distances from the windsock to the edges of the 36 pools divided by the number of pools).

To assess temporal and spatial patterns separately, environmental variables were subdivided into those that varied in time (average and maximal wind speed, wind direction,% calms, number of dry pools, and the total area of exposed propagule bank) and variables that varied in space ('no. pools upwind', 'area reb upwind', 'isolation' and 'near pool'). For the analysis of temporal patterns, yields from different sample periods (T1–T9) were used as replicates (samples from all nine wind socks added up per time interval). For analysis of the spatial patterns, yields from different windsocks (W1–W9) were used as replicates (samples added up per windsock over entire study period).

### *Variation in the structure of the dispersing community*

We investigated whether wind dispersal (total number and richness of propagules and the abundance of different taxa) shows any temporal or spatial patterns and to what extent they can be explained by covarying environmental variables.

To assess whether the structure of the intercepted dispersing community varied in time, we used a multivariate approach and constructed redundancy models based on absolute abundances. Temporal structure of our dataset required the use of a split plot design with the different wind socks as covariables (dummy variables) (Lepš and Šmilauer 2003). Two RDA models were constructed in Canoco for Windows 4.5 (ter Braak and Šmilauer 1998): one with the dummy variable 'time', the second with the environmental variables, as predictors. We opted for RDA rather than canonical correspondence analysis (CCA) since previous detrended canonical correspondence analysis (DCCA) indicated a dominance of linear compared to unimodal gradients. A forward selection procedure was used to maintain only significant explaining variables. Using variation partitioning (Borcard et al. 1992) we compared the amount of variation that was either explained unique or in common by the different environmental variables. When testing unique effects of one variable, all other environmental variables were used as covariables. We remark that the use of the circular variable 'average wind direction' in RDA is not ideal as some subtlety of the variable is lost.

We also constructed RDA models to investigate whether the structure of the intercepted dispersing community showed spatial variation. No split plot design was needed and samples from all time intervals were added up per windsock to investigate whether any differences in collected communities can be attributed to environmental differences related to the location of the windsocks. Again, a forward selection procedure was used in order to maintain only significant explaining variables in the model. Species data were LOG transformed to decrease the impact of abundant taxa relative to rarer taxa.

### *Variation in the total amount and richness of dispersing propagules*

To uncover temporal patterns in the richness and the total amount of caught propagules, we added up the yields of all wind socks per moment and constructed multiple and simple linear regression models using the environmental variables that varied in time as predictor variables. The number of propagules, taxon richness and environmental variables were plotted against time to visualise patterns. As all pools were filled just before t4, two different drying cycles (t1–t3 and t4–t9) were distinguished. Due to mixing of pool sediment during heavy rains, the availability of propagules for wind dispersal changes between cycles, making them difficult to compare. We therefore constructed separate regression models for each cycle. In order to specifically investigate the effect of the circular variable wind direction we used circular statistics (Oriana 2.02: Kovach 2006). A circular-linear correlation coefficient (Zar 1999) was used to calculate correlations between the circular variable wind direction and the linear variables 'taxon richness' and 'no. propagules'. We remark that independent analyses for the two drying cycles, not included in this paper, revealed similar patterns.

To investigate the spatial patterns in the richness and the total amount of caught propagules, we added up the yields in time per wind sock and constructed multiple and simple linear regression models using the different environmental variables that varied in space as predictor variables. To investigate the effect of the dominant wind direction (N) on the number and richness of dispersing propagules we constructed a categorical variable dividing the windsocks into three groups, differing in the number of available potential source pools along the N-S axis. A pool was regarded as a potential source pool when it was situated 'upwind' (i.e. North) from a particular windsock. The three groups consisted of peripheral windsocks (W1, W2, W6, W7) that did not have any pools upwind, central pools (W3, W5, W8) that had one or two pools upwind and finally the downwind pools (W4, W9) that had $>4$ pools upwind. As assumptions of normality were unfulfilled, a nonparametric Kruskal Wallis test was used to investigate differences between groups in taxon richness and the number of intercepted dispersing propagules.

## Results

### Wind speed and direction

Average wind speed during the study period was $2.5 \pm 1.4$ m s$^{-1}$. Wind speed varied from 0 to 9 m s$^{-1}$. Peaks in average wind speed coincided with heavy thunderstorms on 4 August and 24 August (Fig. 3). The dominant wind direction during the entire study period was north, closely followed by north western winds.

### The dispersing community

A total of 850 viable propagules were intercepted including 17 invertebrate taxa (Table 1). The dispersing community was mainly composed of crustacean resting eggs and ephippia. Other dormant propagules consisted of juvenile and adult life stages of harpacticoid copepods, ostracods, nematodes and the locally abundant oribatid mite *Aquanothrus montanus*. We also intercepted one fully intact adult calanoid copepod.

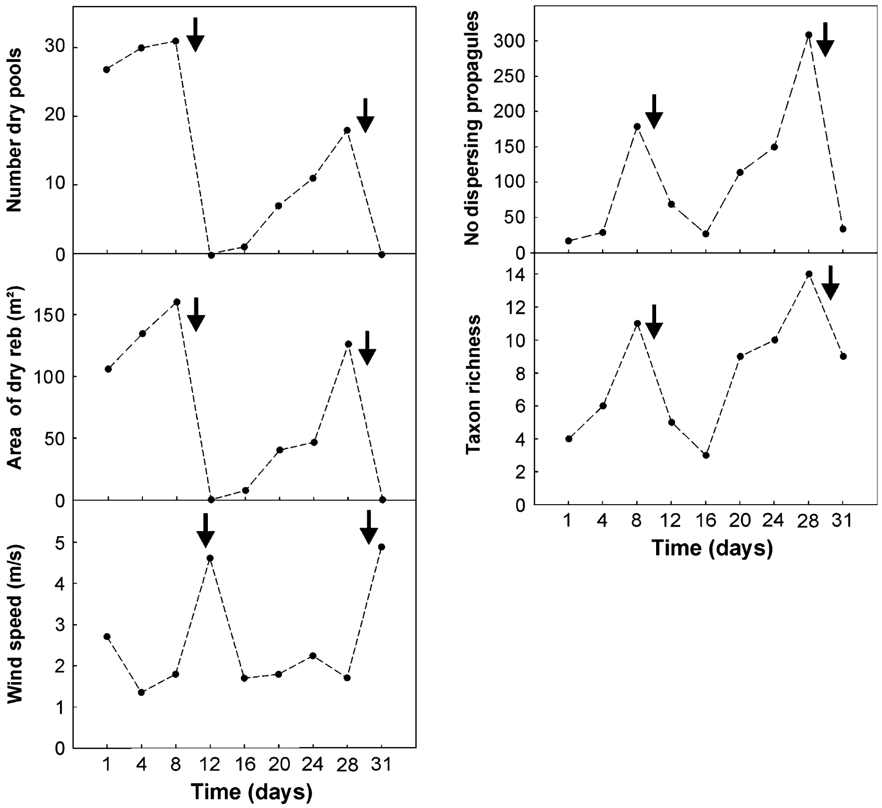

Fig. 3. Temporal variation in the number of dispersing propagules, taxon richness of dispersing propagules, number of dry pools, surface area of exposed propagule bank (area of dry reb) and average wind speed (24 July until 24 August 2006). Arrows indicate two thunderstorms with heavy rains.

## Variation in the structure of the dispersing community

Wind dispersal was variable during the study period. Both time and environmental variables significantly explained some variation (12.9 and 11%, respectively) in the abundances of dispersing invertebrates (Table 2). In a forward selection, only the variables wind speed, wind direction and the area of exposed propagule bank significantly explained some variation in the abundance of taxa.

A forward selection procedure on an RDA revealed no significant spatial effect of environmental variables on the structure of the dispersing communities ($p > 0.05$).

## Variation in the total amount and richness of dispersing propagules

Temporal wind dispersal patterns (no. propagules and richness) closely follow temporal patterns in the number of dry pools and the total area of exposed propagule bank (Fig. 3). These patterns are supported by regression models, but were only significant when both drying cycles were analysed separately (Table 3). Although the observed patterns were the same for both cycles (Fig. 3), we only included models for the second (longest) drying cycle (T4–T9) as regressions based on three data points (first drying cycle: T1–T3) lack sufficient statistical power and are therefore not very meaningful. After step by step removing nonsignificant predictor variables from multiple regression models, only the variable 'number of dry pools' remained significant both as a predictor of richness and of the number of intercepted propagules, explaining 87% and 71%, respectively. No significant correlations were found between

Table 1. List of invertebrate taxa collected in the wind socks and number of individuals collected for each taxon.

| Group | Taxon | No. propagules |
|---|---|---|
| Resting eggs | | |
| Anostraca | *Branchipodopsis tridens* | *44* |
| Spinicaudata | *Leptestheria striatoconcha* | *9* |
| Cladocera | *Macrothrix propinqua* | *6* |
| | *Chydorus sphaericus* | *44* |
| | *Alona costata* | *68* |
| | Chydorid type B | *3* |
| | Chydorid type D | *3* |
| | Chydorid type E | *3* |
| Turbellaria | sp. | *14* |
| Copepoda | *Calanoida* sp. | *204* |
| Other (cryptobiotic) life stages | | |
| Bryozoa | sp. | *13* |
| Copepoda | *Harpacticoida* sp. | *390* |
| | *Calanoida* sp. | *1* |
| Ostracoda | *Korannacythere devriesi* | *26* |
| | *Heterocypris* sp. | *2* |
| Oribatidae | *Aquanothrus montanus* | *11* |
| Nematoda | sp. | *9* |

Table 2. RDA models (999 permutations, split plot design) explaining the community structure (absolute abundances of taxa) of collected propagules on different moments in time using the dummy variable 'time' and respectively the environmental variables average wind speed, average wind direction and the area of exposed dormant propagule bank ('area reb') as predictor variables. Different variance components are distinguished: the unique variance explained by 'avg wind speed', 'avg wind direction' and 'reb area', the variation they explain in common and the unexplained variation.

| Analysis | Predictor variables | % variance explained | F-ratio | p |
|---|---|---|---|---|
| RDA | time | 12.9 | 1.625 | 0.001 |
| RDA | full model | 11 | 5.009 | 0.001 |
| | avg wind speed (m s$^{-1}$) | 3.7 | 5.154 | 0.004 |
| | avg wind direction (°) | 2 | 2.741 | 0.016 |
| | reb area (m$^2$) | 2 | 2.146 | 0.002 |
| | unexplained | 87 | | |
| | commonly explained | 5.3 | | |

average wind direction and number ($r = 0.314$; $p = 0.553$) and taxon richness ($r = 0.376$; $p = 0.426$) of dispersing propagules.

The number and richness of intercepted propagules also varied in space. Regression models (Table 4) show significant positive effects of the predictor variables 'no. pools upwind' and 'area reb upwind' on the response variables taxon richness and the number of dispersing propagules intercepted by each windsock, respectively. When all variables were integrated in a multiple regression analysis, only the variable 'area reb upwind' remained significant and explained 85% of variation in taxon richness and 82% of variation in the total number of intercepted propagules.

Additionally, the amount of intercepted propagules and the richness was higher in the 'downwind' windsocks than in the 'peripheral' windsocks (Fig. 4, Table 4). This relationship was marginally significant for the number of propagules (Kruskal Wallis, $p = 0.055$) and significant for the taxon richness (Kruskal Wallis, $p = 0.048$).

## Discussion

Contrary to previous studies (Jenkins and Underwood 1998, Brendonck and Riddoch 1999, 2000a) we found direct evidence that a large number of aquatic invertebrates (17 taxa) readily disperse by wind and that this process is frequent, even over a short period of time (one month). In contrast to what the findings in Brendonck and Riddoch (1999, 2000a) suggest, we showed here that different dormant propagules can easily be lifted to at least 1.5 m.

### The limiting effect of propagule bank exposure

Both the structure of the dispersing community as well as the taxon richness and the total number of intercepted propagules varied during the one month sample period. There were no significant spatial effects on the structure of the dispersing communities. This is not surprising considering the limited number of replicate observations (nine windsocks), hence low statistical power. We were able to explain 11% of the variance in abundances of different taxa using the variables 'average wind speed', 'average wind direction' and the 'area of exposed propagule bank'. Moreover, regression models indicated that wind dispersal increased when pools dried up and that the number of dry pools was the most important factor, significantly explaining 71% of the taxon richness and 87% in the total number of dispersing propagules. Changes in the collected propagule community structure with time may result from differences in wind direction between time intervals, promoting dispersal from different source pools that often housed largely different communities (Vanschoenwinkel et al. 2007). Temporal changes may also result from variable wind speed that may variably launch different propagules from the propagule bank depending on differences in critical wind speed of different egg types (threshold friction velocity TFV; Gillette 1978). The strong effect of propagule bank exposure on the collected propagule community indicates that the temporally variable presence of water greatly inhibits the dispersal of propagules from the propagule bank. We must remark that we also collected propagules when all pools were wet after rains (t4). As the rainfall only started 12 hours after the start of this time interval it is possible that some dispersal from dry pools had already occurred. On the other hand, at least part of the

Table 3. Linear regression models with temporally varying environmental variables as predictor variables and the number and taxon richness of dispersing propagules as response variables, respectively (sample periods were used as replicates). Models were based only on observations from the second drying cycle (T4–T9).

| Simple regression | Taxon richness | | | No. propagules (log) | | |
|---|---|---|---|---|---|---|
| | ß | p | R$^2$ | ß | p | R$^2$ |
| Avg wind speed (log) | −0.22 | 0.679 | 0.047 | −0.35 | 0.492 | 0.125 |
| Max wind speed | −0.1 | 0.854 | 0.01 | −0.02 | 0.964 | 0 |
| % calms | 0.31 | 0.556 | 0.093 | 0.41 | 0.425 | 0.165 |
| No. dry pools | 0.84 | 0.035 | 0.712 | 0.93 | 0.007 | 0.866 |
| Area reb | 0.83 | 0.04 | 0.69 | 0.89 | 0.017 | 0.795 |

Table 4. Linear regression models with spatially varying environmental variables as predictor variables and the number and taxon richness of dispersing propagules as response variables, respectively (wind socks were used as replicates).

| | Taxon richness | | | No. propagules (log) | | |
|---|---|---|---|---|---|---|
| | ß | p | $R^2$ | ß | p | $R^2$ |
| No. pools upwind | 0.76 | 0.018 | 0.57 | 0.84 | 0.005 | 0.71 |
| Area dry reb upwind ($m^2$) (log) | 0.92 | 0.025 | 0.85 | 0.90 | 0.0007 | 0.82 |
| Isolation (m) | 0.17 | 0.653 | 0.03 | 0.46 | 0.21 | 0.212 |
| Nearest pool (m) | 0.24 | 0.537 | 0.06 | 0.42 | 0.26 | 0.17 |

resting egg bank of anostracans (Brendonck et al. 1998), rotifers and cladocerans (Brendonck and De Meester 2003) is known to float upon rehydration and may be removed by winds when pools are filled. Field observations on our study site indicate that at least part of the resting bank of the anostracan *Branchipodopsis tridens* also floats after inundation (Vanschoenwinkel unpubl.). As dispersing eggs of *B. tridens* were only caught when pools were dry this may indicate that the surface tension of water may be too strong for floating propagules to be picked up by wind, at least under the wind speeds observed during our study. Peaks in wind speed did not coincide with wind dispersal peaks (Fig. 3). As strong winds were usually accompanied by heavy rains, the building up of a water layer may have sheltered the dormant propagule bank from winds. Another possible explanation is that short term gusts, important for wind dispersal, are obscured by averaging wind dispersal over longer intervals (Nathan et al. 2005). It is also possible that the naturally occurring wind speeds are not limiting for wind dispersal. High wind speeds were also not a prerequisite for wind dispersal in a terrestrial mite (Duffner et al. 2001). Finally, Tackenberg et al. (2003) concluded that horizontal wind speed, as measured in our study, is not that important for wind dispersal of seeds compared to vertical updraft.

## The importance of dominant winds

Direction of aerial transport is typically constrained by wind direction. Therefore the presence of prevailing winds may limit the possible aerial dispersal interactions between pools in the metacommunity. Although in our study average wind direction had little effect on wind dispersal, the dominant wind direction had an indirect spatial effect: windsocks with most potential upwind source pools and a large upwind area of propagule bank, intercepted more propagules as well as a higher richness of taxa (regression models in Table 4), resulting in assymetrical dispersal. As dominance of certain wind directions occurs in many parts of the world, this variable should therefore be taken into account, e.g. to predict the spread of invasive species (Kellogg and Griffin 2006) or to relate patterns of genetic differentiation to aerial dispersal pathways.

During the second of two drying cycles, a larger number of dormant propagules (per yield) was collected than during the first (Fig. 3) although a larger fraction of pools was dry during the first dry spell. Also, regression models only fitted the observed temporal pattern when both cycles were treated independently. This may point at the importance of sediment mixing after rains (T3) increasing the availability of loose propagules for wind dispersal. During the first observation period the superficial layer of dispersal prone propagules most probably was already exhausted due to the prolonged dry period (several months) anticipating the first collections. The drying sequence of pools in both cycles was virtually identical so that this did not interfere with the observed pattern. Wind patterns (direction and speed) were also comparable between the two cycles. We also remark that due to subfreezing night temperatures and short duration of inundation there was no production of propagules in the flooded pools.

## An alternative view of source-sink dynamics?

In source-sink metapopulations large habitat patches are typically considered as sources and smaller habitat patches

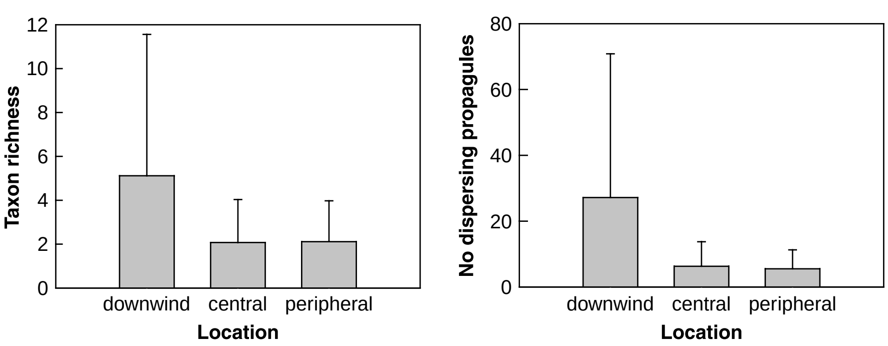

Fig. 4. Means and standard deviations of taxon richness and number of dispersing propagules intercepted by windsocks with a different number of potential source pools for aerial dispersal (relative to the dominant wind direction north). peripheral: 0; central: 1–2 and downwind: >4 potential source pools.

as sinks (Levin 1974). However, this general idea may not apply for temporary aquatic habitats. As immediately after drying the amount of propagules available for dispersal is maximal, this may have consequences for the amount and direction of dispersal among different types of pools. Because they dry up more often, smaller pools with short inundation cycles (even though egg banks in these systems are probably smaller) may contribute more and more frequently to wind dispersal than larger pools that only dry up once each season. Propagules dispersing from dry pools also have a better chance to successfully colonise still flooded pools as water is more efficient in retaining incoming dispersing propagules than a dry pool basin. The combination of both effects may lead to an alternative view of source sink dynamics with smaller and more frequently drying pools being the best 'sources' and larger pools being the best 'sinks' for wind dispersal. A consequence of this mechanism may be that in landscapes where temporary and permanent ponds occur close together, dispersal from temporary to permanent ponds may actually be much higher than vice versa.

## Temporary vs permanent habitats

Due to differences in exposure of the egg bank, the relative importance of wind dispersal compared to other vectors (animals, water) will likely differ between permanent and temporary aquatic systems. During a whole year of collection, Jenkins and Underwood (1998) only collected bdelloid rotifers in their wind socks, but no other (larger) taxa. They placed two wind socks at respectively 150 m and 400 m of a permanent source pond, compared to a maximal distance of less than 16 m in our study. Besides the much higher isolation, the smaller number (two vs nine), smaller diameter (9.5 vs 30 cm) and greater height from ground level (2.5 m and 11 m vs 1.5 m) of their wind socks compared to ours can also contribute to the observed differences. Permanence of the aquatic phase is probably the other main factor explaining their low yield of propagule numbers and richness.

In theory, for permanent water bodies that do not undergo drastic water level fluctuations, the area of exposed propagule bank is very limited and therefore the amount of propagules that is readily available for wind dispersal is lower, although wind dispersal of floating propagules cannot be entirely excluded. At our study site, many pools are dry for most of the year, water connections are rare (and of a temporary nature: Vanschoenwinkel et al. 2007) and animal vectors are absent (water birds) or scarce (amphibians). Under such conditions, wind most likely is the dominant dispersal vector. In permanent waters, on the other hand, directional dispersal via waterways and animal vectors is expected to be more efficient and of higher importance than wind dispersal.

## Impact of erosion

Despite the benefits associated with successful long range dispersal (mediating gene flow among isolated populations and colonisation of habitat patches), wind is expected to be less efficient compared to directional dispersal vectors (animals, water ways) in hitting suitable habitats. Although resting eggs might make repeated movements from suboptimal terrestrial habitats, only a minor fraction of the uplifted propagules will ultimately successfully disperse to another habitat patch (Bilton et al. 2002). The prolonged exposure of the dormant propagule bank to wind action therefore primarily has to be considered a loss factor in the egg bank budget. Especially in ephemeral pools that are dry most of the year, wind erosion can potentially lead to a drastic reduction or even depletion of the dormant propagule banks, reducing the buffering capacity against catastrophes (Warner and Chesson 1985, Brendonck and Riddoch 2000b).

## Wind as a local driver of species sorting processes

Taking into account the short duration of the observations and the nearly infinitesimal air-volume sampled, our findings suggest frequent dispersal by wind of a multitude of invertebrate taxa over at least short distances. This confirms the suggestion in Vanschoenwinkel et al. (2007) that wind dispersal probably is an important local structuring factor in this rock pool metacommunity. The strong observed relation between local environmental conditions and local communities in that study indicated that dispersal was not limiting and that species were sorted among patches using the local environment as a filter. As animal vectors were absent (water birds) or scarce (amphibians) and overflow dispersal only occurred between a limited number of connected pool pairs, we conclude that local wind dispersal most likely is the dominant dispersal agent within the metacommunity. Wind dispersal can here be visualised as a variable heterogenous local cloud of airborne propagules, from which a fraction precipitates on the study site, providing the fuel for species sorting processes that ultimately shape the structure of the local communities (Vanschoenwinkel et al. 2007).

## From local to long distance wind dispersal

Current evidence for effective long distance wind dispersal of aquatic invertebrates remains scarce. During our study only propagules from taxa that were present in the local metacommunity were intercepted so we have no indication for any long distance dispersal. This was expected, as both the time span and the sample intensity of our study were limited. Low efficiency of wind as a dispersal vector makes sure that the probability of successful dispersal over short time scales is most likely low (Jenkins and Underwood 1998, Bohonak and Jenkins 2003), but not necessarily negligible over long time periods. In that respect, the presence of a large diversity of passively dispersing invertebrates in pools on isolated mountaintops, as the ones in this study, in the absence of suitable dispersal vectors such as water birds, may be indicative for the effectiveness of long distance wind dispersal over long time scales. More research, however, will be necessary to unravel to what extent local wind dispersal rates relate to long distance dispersal and colonisation. Bacteria and fungi are known to disperse between continents in dust clouds generated by storm activity over deserts (Kellogg and Griffin 2006). No such records exist of metazoan propagules. Nathan et al. (2002) suggested that the possibility of long distance wind dispersal by seeds is determined by local turbulent airflows and the potential to take off or land. Additionally large eddy simulations have shown that depressions in the landscape such as forest openings can act as efficient points for both pick up and deposition of propagules (Nathan et al. 2005). Consequently, wind dispersal may be less stochastic than previously thought, and it remains to be studied whether pool depressions may serve a similar function.

## Conclusions

Passive wind dispersal of freshwater invertebrates occurred frequently on our study site and exposure of the dormant propagule bank was the most important factor limiting wind dispersal. Temporal variation in wind speed was much less important. We found an indirect effect of dominant wind direction, by determining the number of potential sources for dispersal. Wind dispersal is generally considered to be of little importance, especially in permanent waters, when compared to the directional dispersal associated with animal vectors or running water. In some (especially temporary) aquatic systems, where other dispersal vectors are scarce or absent, wind can be important, not only as a dispersal vector but also through erosion of the dormant propagule bank. In relation to a previous paper (Vanschoenwinkel et al. 2007) we conclude that wind dispersal is a key factor, driving species sorting processes in this metacommunity. It is yet to be studied how local wind dispersal rates relate to long distance wind dispersal.

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