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Temporal and spatial variation in temperature and oxygen at the microscale: key niche axes for aquatic life

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To understand animal adaptations, we need accurate estimates of the ecological factors impacting organisms in nature. While temperature is a well-established driver of physiological performance, its effects in aquatic systems are closely linked to water oxygenation. Oxygen levels are expected to differ spatially and fluctuate temporally much more strongly in water than on land, but our understanding of variation in temperature and oxygen levels in freshwaters remains limited. It is essential that environmental variation is recorded at spatial and temporal resolutions relevant to the organism. Here, we analyse spatial and temporal variation in water temperature and oxygenation across running and standing waters, using both microscale spot measurements and continuous loggers collecting data from the water column. Our results reaffirm that small-scale thermal gradients are much less pronounced in water than on land due to the high thermal conductivity and heat capacity of water. Regional weather conditions can therefore reliably predict water temperature across scales. By contrast, oxygen levels are much harder to predict from large-scale data as they can fluctuate sharply over very small spatial scales and within a single day, particularly in standing waters, exposing aquatic organisms to steep oxygen gradients. Our findings underscore the importance of incorporating fine-scale oxygen dynamics when studying aquatic species distributions and ecological strategies.

This article is part of the theme issue 'Life in natural microcosms'.

1. Introduction

Organismal fitness varies across environmental gradients, and temperature is a key variable directly impacting physiological rates, with a substantial body of research exploring thermal responses in performance, mostly through laboratory studies [1–3]. In water, thermal responses are modulated by water oxygenation, affecting organismal survival [4], body size [5] and distributional ranges [6]. To understand species–environment relationships and predict species responses to environmental change, it is essential to quantify the environmental conditions experienced by organisms in nature [7]. In his 1977 presidential address to the BES, Southwood argued that the habitat could be considered as the templet on which ecological strategies were forged and emphasized the importance of measuring at relevant spatial and temporal scales, by relating the scale of the measurements to the generation time and movements of an organism [8]. Herein lies a challenge, as the spatial and temporal resolution of environmental data is frequently much more coarse-grained compared with scales that are relevant for individuals in nature [9]. Although there is broad recognition of the need to incorporate habitat characteristics at finer scales to answer ecological and biogeographical

questions at local, regional and even larger scales [7,10,11], such data are often lacking or difficult to obtain, particularly in aquatic systems.

Most work on habitat conditions at the microscale has been performed on land. Here, small-scale variations in temperature, humidity and solar radiation can be substantial, mediated by differences in topography, vegetation and soil type. These factors are often considered together as the microclimate, given the strong interactive effects of air humidity, temperature and insolation. In arthropods, for example, air temperature modulates water balance [12], while moisture modulates thermal preference [13]. In water, the high conductivity and heat capacitance of water reduce the opportunities for fine-scale spatial variation in temperature compared with on land. Most work on thermal variation in freshwater ecosystems relates either to vertical clines due to lake stratification or temporal variation in water temperature, and very few studies have focused on thermal variation in the shallow littoral zones of freshwater ecosystems [14–17]. Oxygenation, already mentioned as an important modulator for thermal responses of aquatic organisms, can exhibit substantial spatial variation in aquatic ecosystems, contrasting with the situation on land, where oxygen levels are much more invariant. For example, strong diurnal fluctuations in oxygen levels have been documented in shallow freshwater ecosystems [18–20].

Given the importance of the coupling between water temperature and water oxygenation for aquatic organisms, we investigated spatial and temporal variation in both water oxygenation and temperature across running (two sites) and standing waters (two sites) in southern Britain. We compare and measure temperature and oxygen at the microscale using spot measurements and at the scale of the waterbody using data loggers. We explore how time of day and season drive variation in both temperature and oxygen, and whether their impacts differ for running and standing waters. We also ask to what extent small-scale variation can be predicted from coarse-resolution data, by relating microhabitat variation in temperature and oxygen to measurements from the water column and to regional weather data. Our study characterizes oxygen conditions at the microhabitat scale across running and standing water bodies and how the dynamics and its predictability differ from those of water temperature.

2. Methods

(a) Data collection

Data were collected in four different water bodies (i.e. sites), two running and two standing (electronic supplementary material, figure S1). These were all located on private lands in Devon (UK, 50°29′N 3°48′W). Running waters were the river Mardle, which originates on Dartmoor and discharges into the river Dart, and a small first-order stream, which discharges into the river Mardle. Standing waters comprised a duck pond in a forest and a sun-exposed reservoir, both close to Buckfastleigh. Handy Polaris Loggers (OxyGuard) were deployed at each site. Periodically, these were retrieved, read out, calibrated, serviced and redeployed during the period from 23 December 2011 to 17 July 2012. Loggers were placed such that they measured the oxygen conditions in the water column, 5–10 cm above the sediment, at a depth of 20–40 cm (note that this is equivalent to the open water microhabitat sampled below).

We also performed spot measurements to characterize microhabitat conditions during five field visits (electronic supplementary material, table S1). On each visit, water temperature and water oxygenation were measured across representative microhabitats in each site. Typically, 3–5 microhabitats would be measured, and each type of microhabitat would be measured at five different spots in the waterbody (i.e. replicates) in the morning and in the afternoon (two sampling times). Spot measurements were made in the littoral zone at a depth up to approximately 40 cm, and replicate measurements were made in close proximity to one another (within a few metres along the shoreline). Since all four water bodies were quite shallow (<2 m), no attempt was made to characterize the vertical gradient. Instead, measurements were focused on the shallow, littoral zone, where insolation is highest and where the vast majority of macroinvertebrates reside. Over these five field visits, we collected 775 spot measurements (3–5 microhabitats × morning and afternoon × five replicates × four sites × five visits). We used a battery-powered, portable Fibox 3 LCD Trace oxygen meter with a temperature sensor and a DP-PST3 optical oxygen sensor, the end of which is covered in a steel tube to protect both the sensor material and the optical fibre (PreSens GmBH, Germany).

We retrieved weather data on daily temperature and cloud cover from a nearby weather station (Teignmouth) via the Met Office MIDAS Open website [21]. Rainfall data were sourced from the HadUK-Grid Gridded Climate Observations [22], extracting the rainfall data from the 1 km^2 grid that encompassed our study area and also the four adjacent 1 km^2 grids, and these data were then averaged.

(b) Data analyses

To evaluate variation in spot measurements of water temperature and oxygenation at the microscale, we ran models that included as fixed factors: Julian day (as a proxy for seasonal change), time of day (morning or afternoon), site and microhabitat. In addition, we allowed for time of day to vary across sites and microhabitats by including the appropriate interactions. We ran the same model for water temperature and oxygen, so we could evaluate the relative contribution of the different fixed factors.

To evaluate temporal variation in logger data for water temperature and oxygenation across sites, we ran models that included as fixed factors weather conditions, site and time of day (as a continuous variable). Weather conditions included air temperature, cloud cover and rainfall, averaged over the last five days. Preliminary analysis also tested whether five-day averages for air temperature and cloud cover improved model performance. We included the appropriate interactions to allow the effects of weather conditions and site to vary with time of day. In addition, weather conditions were allowed to affect water

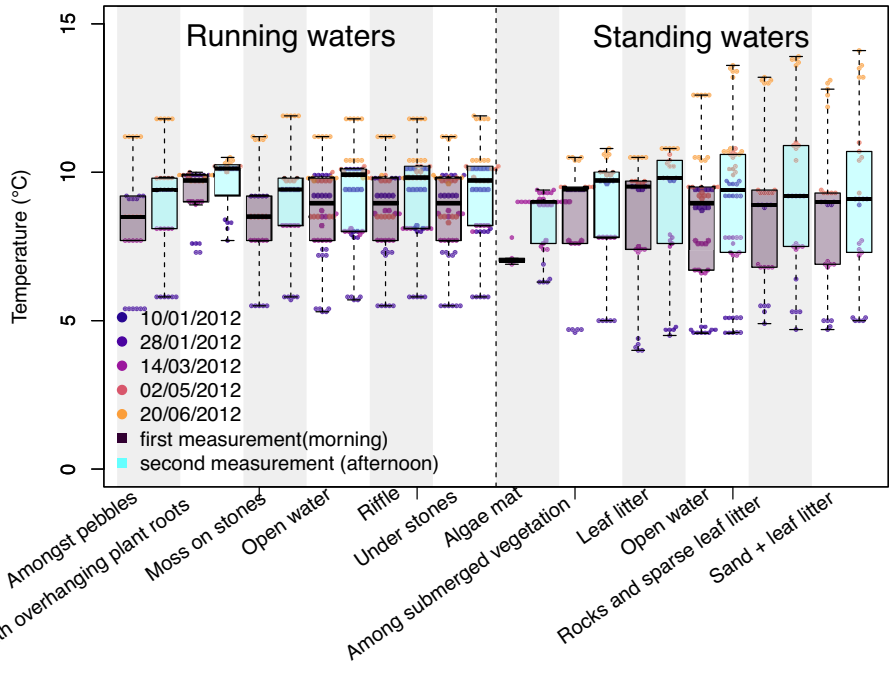

Figure 1. Microhabitat temperature measured in the morning or afternoon at different microhabitats and at different sites (two running water sites and two standing water sites).

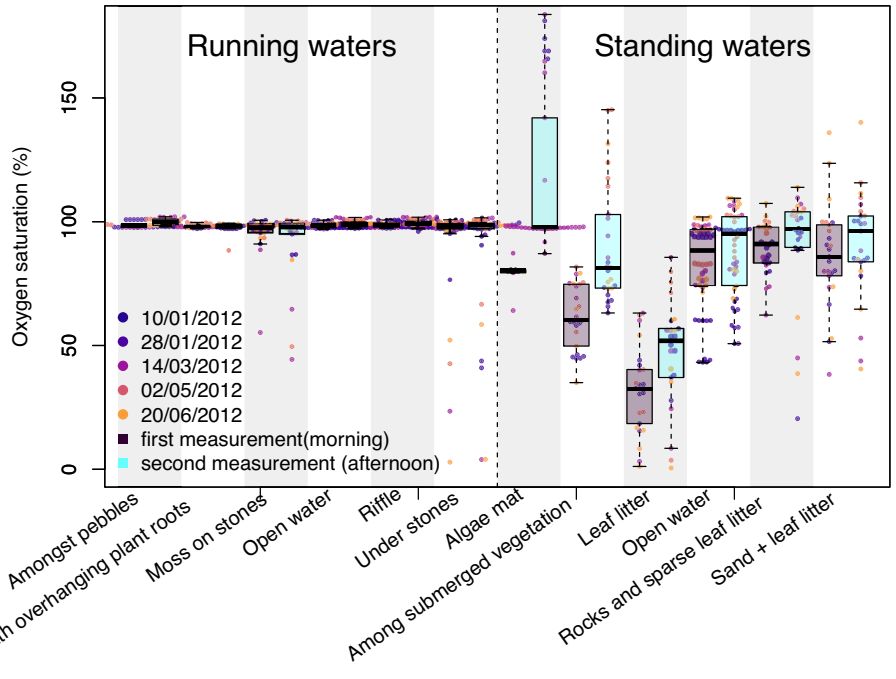

Figure 2. Microhabitat oxygen saturation measured in the morning or afternoon at different microhabitats and at different sites (two running water sites and two standing water sites).

temperature and oxygenation differently across sites. We constructed temporal variograms by calculating correlations between water temperature and dissolved oxygen measurements taken at the same location but separated by varying time lags. Ten time lags were used, increasing in length by approximately a factor of two: 15 min, 30 min, 1 h, 3 h, 6 h, 12 h, 1 day, 3 days, 1 week and 2 weeks. To test how well variation in temperature and oxygen at the microhabitat level can be predicted from coarser resolution data, we first tested the relationships between microhabitat spot measurements and logger data, selecting, for each timepoint, the microhabitat that was measured, the corresponding reading from the logger for that day and site. Next, we fitted simple linear models relating spot measurements to logger data for both water temperature and oxygenation. We then ran the same models on either the two running water sites or the two standing water sites to evaluate the effect of water body type. To test for potential measurement differences across equipment, we also compared spot measurements obtained for the open water microhabitat (i.e. near the location at which the loggers were deployed) with the data as recorded by the loggers. Finally, variation in spot measurements at the microhabitat level was related to weather conditions. To do so, we included water temperature or water oxygenation (spot measurements) as dependent factors and weather conditions, time of day and their

Table 1. Type III ANOVA results for the model relating variation in microhabitat temperature to season (Julian day), time of day, site and microhabitat, including their interactions.

predictor	sum sq.	d.f.	*F* value	*p*-value
(intercept)	506.34	1	286.02	<0.001
Julian day	1206.51	1	681.53	<0.001
time of day	17.88	1	10.10	0.0015
site	38.21	3	7.20	<0.001
microhabitat	55.15	10	3.12	<0.001
time of day × site	62.83	3	11.83	<0.001
time of day × microhabitat	41.19	10	2.33	0.0106
residuals	1320.65	746		

Table 2. Type III ANOVA results for the model relating variation in microhabitat oxygen saturation to season, time of day, site and microhabitat, including their interactions.

predictor	sum sq.	d.f.	*F* value	*p*-value
(intercept)	75 055	*1*	332.90	<0.001
Julian day	1513	1	6.71	*0.0098*
time of day	14 156	*1*	62.79	<0.001
site	15 700	3	23.21	<0.001
microhabitat	38 205	10	16.95	<0.001
time of day × site	233	*3*	0.34	0.7932
time of day × microhabitat	18 841	10	8.36	<0.001
residuals	168 191	746		

interaction as fixed factors. We also tested whether including site identity and all two-way interactions further improved model fits. All analyses were performed using R Statistical Software [23]. For oxygen conditions, we focused our analysis on per cent saturation (i.e. 100% saturation ≅ 21 kpa), rather than dissolved oxygen (moles per litre), as the effects of temperature on oxygen solubility are already accounted for when expressing oxygen conditions in this manner [24].

We also translated the observed variation in water temperature and dissolved oxygen into estimated changes in organismal performance. For temperature, we applied a simple Q_{10} relationship (Q_{10} was set to 2, meaning that a 10°C increase would result in a twofold increase in performance), with performance set to 100% at the mean temperature. For oxygen, we related performance directly to oxygen saturation, assuming the focal species to be an oxyconformer [25]. We acknowledge that these are simplified approximations and that the precise responses to temperature and oxygen will vary across species. Nevertheless, as an initial approach, this provides a useful first-order insight.

3. Results and discussion

(a) Microhabitat conditions (small-scale spatial variation)

Across the research period, large differences were recorded for both temperature (min: 4.0°C; max: 14.1°C) and oxygen saturation (min: 0.52%; max: 183.7%). However, microhabitat variation was partitioned very differently for either temperature or oxygen (figures 1 and 2). Variation in temperature was driven predominantly by seasonal differences (Julian day) and much less by diurnal differences and differences across sites (table 1). In contrast, variation in oxygen saturation was predominantly driven by diurnal differences (i.e. whether measurements were taken in the morning or in the afternoon), especially in standing waters. Here, decomposition processes consuming oxygen and photosynthesis generating oxygen resulted in larger diurnal fluctuations, with oxygen saturation sometimes exceeding 100% (i.e. becoming supersaturated). We also found a strongly significant interaction between time of day and microhabitat (table 2), indicating that such daily fluctuations in oxygen were more pronounced in some microhabitats in standing waters (e.g. submerged vegetation; figure 2). In running waters, both rates of decomposition and photosynthesis were likely reduced (algae and leaf litter are continuously transported downstream, rather than accumulating), and fluctuations in oxygen saturation are further reduced due to the continuous mixing and (re-)aeration in flowing conditions. In addition, there were consistent differences across the different microhabitats sampled (site; table 2). This means that while benthic aquatic invertebrates do not encounter strong thermal gradients on a given day, oxygen gradients may be strong across relatively small distances, especially in standing waters (e.g. moving from a leaf pack to an algal mat). These distances can be as small as a few centimetres when comparing the inside of a leaf pack with the overlying

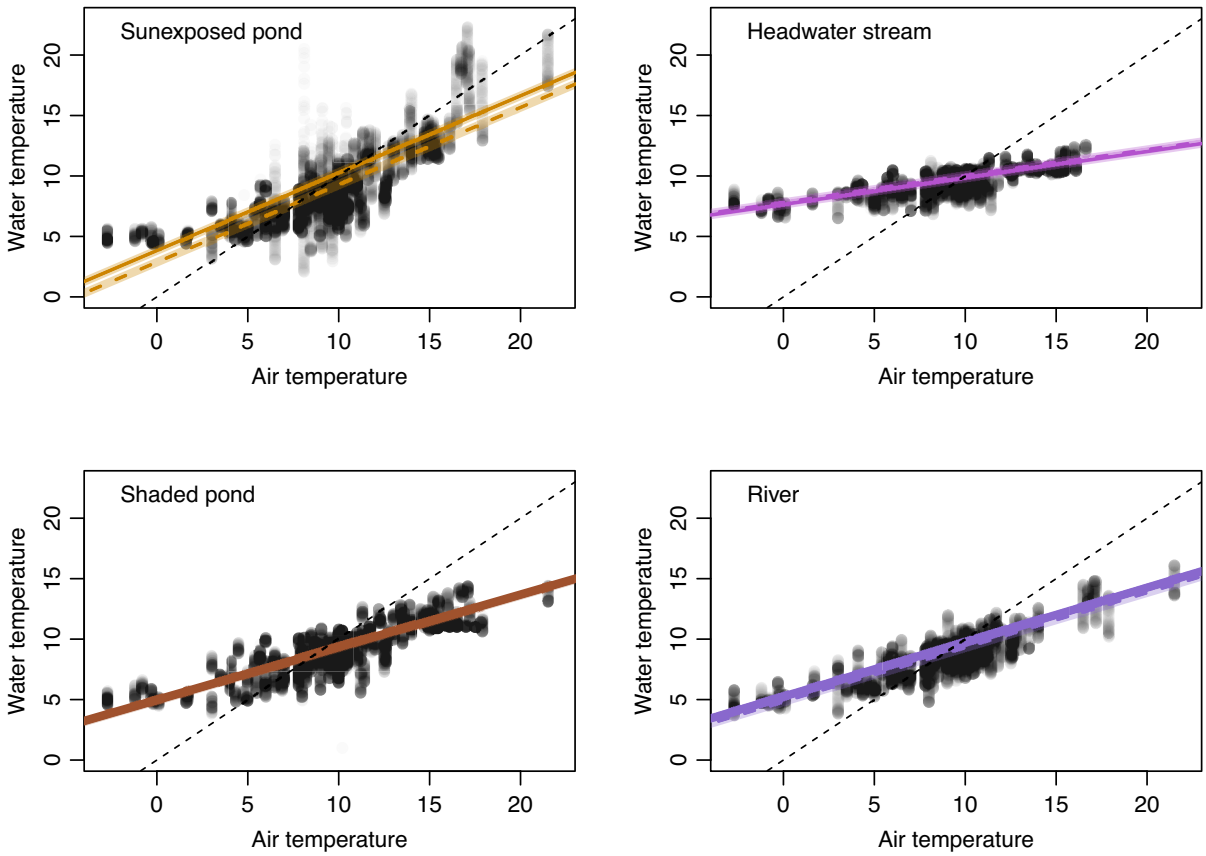

Figure 3. Logger temperature data, plotted against air temperature for each of the four sites separately. Note that the two standing waters are plotted on the left, while the two running waters are plotted on the right. Solid lines indicate days with low cloud cover and no rainfall, while dashed lines indicate days with high cloud cover and rainfall.

algal mat and may mean the difference between severe hypoxia and physiologically challenging hyperoxia. In running waters, differences in oxygen and temperature are smaller, but occasionally we measured lower oxygen saturation under stones, presumably when leaf litter accumulated and obstructed flow and/or reduced oxygen locally due to decompositional processes. Again, the distances involved are small (<10 cm), and stream invertebrates are sufficiently mobile to escape from putative hypoxic stress in these situations by selecting more exposed microhabitats with higher flow, which they readily do [26,27]. Taken together, this strongly contrasts with the situation on land, where oxygen clines are virtually absent, but short distances may feature strong thermal gradients [10,11].

(b) Logger data (large-scale temporal variation)

The logger data (electronic supplementary material, figure S2) show that water temperature varies predictably, largely as a function of air temperature (figure 3). Strong relationships between air temperature and water temperature are frequently reported [28], but the exact relationship differs from water body to water body depending on volume, flow, insolation and seepage. For example, our first-order stream is notable for being least responsive to air temperature, likely because water temperatures are buffered by seepage of groundwater. Differences in rainfall and cloud cover only lead to an appreciable increase in water temperatures in the sun-exposed pond. In contrast, levels of oxygen saturation were affected by air temperature to a much lesser degree (electronic supplementary material, figure S3).

We measured pronounced diurnal variation in oxygen saturation in standing waters, especially in the sun-exposed pond (figure 4). Diurnal variation in temperature was much smaller (electronic supplementary material, figure S4). Variation in water temperature could be reasonably accurately modelled from information on weather, site and time of day (R^2 = 72.1%; table 3), whereas for oxygen saturation the explained variation was lower (R^2 = 63.6%; table 4). Moreover, air temperature was the strongest predictor for variation in water temperature (already explaining 60.9% of the variation in water temperature by itself), whereas for water oxygenation, differences between water bodies and their diurnal rhythm were more important. Since water temperatures were strongly related to air temperature, it is possible to downscale and model water temperature accurately from larger scale predictors. Global maps of freshwater temperature have been constructed and used to predict range limits in fish and geographical variation in amphipod performance [29,30]. Generating such models for water oxygenation will be more difficult as variation in water oxygenation was largely dependent on site-specific characteristics (table 4). Thus, oxygen levels are affected by differences between sites such as sun exposure, seepage, thickness of leaf litter, nutrient input and primary productivity, as well as the differences between running and standing waters mentioned above. A fruitful direction for future research would therefore be to expand this type of work to include more water bodies and relate site-specific characteristics to their oxygen regimes in more detail.

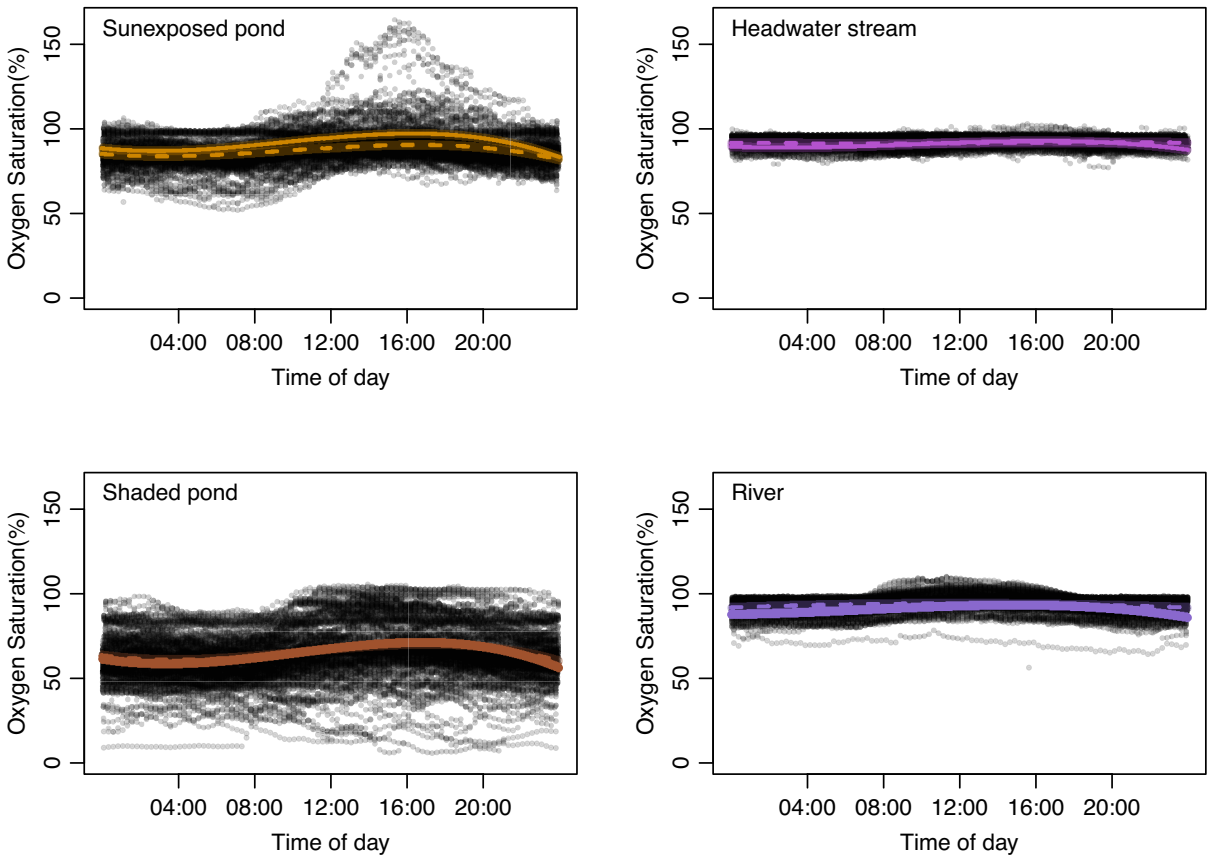

Figure 4. Logger oxygen saturation data, plotted against time of day for each of the four sites separately. Note that the two standing waters are plotted on the left, while the two running waters are plotted on the right. Solid lines indicate days with low cloud cover and no rainfall, while dashed lines indicate days with high cloud cover and rainfall.

Table 3. Type III ANOVA results for the model relating variation in logged water temperature to differences across sites and time of day (time, modelled as a third degree polynomial), and differences in weather conditions (air temperature, cloud cover, rainfall), including their interactions.

predictor	sum sq.	d.f.	*F* value	*p*-value
(intercept)	20 498	1	14 089.23	<0.001
site	7135	3	1634.75	<0.001
time (polynomial, d.f. = 3)	1057	3	242.14	<0.001
air temperature	87 726	1	60 299.34	<0.001
cloud cover	2144	1	1473.52	<0.001
rainfall (lag 5 days)	7	1	5.12	0.0237
site × air temperature	17 245	3	3951.25	<0.001
site × cloud cover	1666	3	381.71	<0.001
site × rainfall	599	3	137.14	<0.001
time × air temperature	481	3	110.24	<0.001
time × cloud cover	577	3	132.15	<0.001
time × rainfall	207	3	47.32	<0.001
site × time	744	9	56.80	<0.001
residuals	77 417	53 213		

Temporal variograms assess the autocorrelation in the data by calculating correlations between water temperature and dissolved oxygen measurements taken at the same location but separated by varying time lags (figure 5). These show that the ability to predict oxygen saturation from prior measurements decays faster than for temperature. Within 12 h, predictability for oxygen saturation drops below 50% in all four sites, while predictability for temperature is above 50% for up to a week. At exactly 24 h, the explained variation increases, as it is then in sync with the diurnal fluctuations, and as we have seen above, this effect is stronger for oxygen saturation than for water temperature. This means that not only are there more factors involved in driving oxygen dynamics compared with temperature dynamics (which is largely governed by air temperature), but these also likely act over shorter time scales.

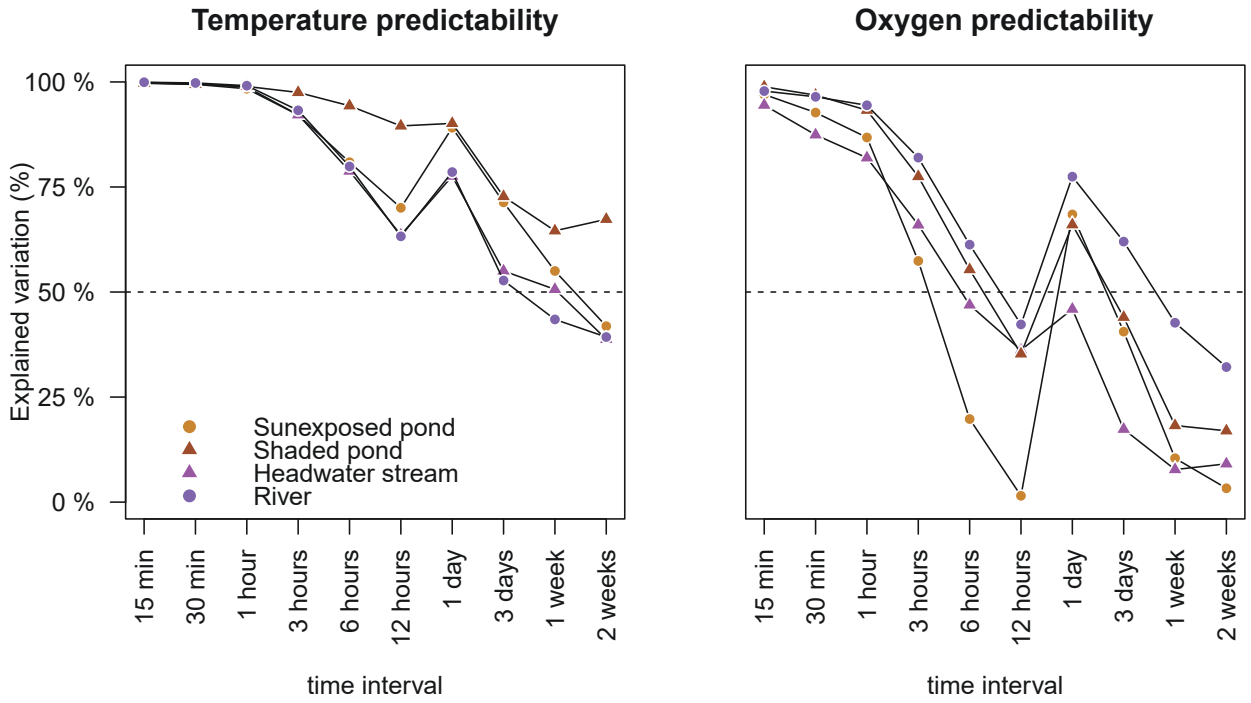

Figure 5. Temporal variograms showing the explained variation when correlating measurements of water temperature (left panel) and oxygen saturation (right panel) taken at the same location but separated by varying time lags. Each site is indicated by a separate line and symbol. The time lags are chosen such that they increase in length by approximately a factor of 2 (see Methods).

Table 4. Type III ANOVA results for the model relating variation in logged water oxygen saturation to differences across sites and time of day (time, modelled as a third degree polynomial), and differences in weather conditions (air temperature, cloud cover, rainfall), including their interactions.

predictor	sum sq.	d.f.	*F* value	*p*-value
(intercept)	9 597 610	1	97 914.62	<0.001
site	1 048 381	3	3565.19	<0.001
time (polynomial, d.f. = 3)	40 885	3	139.04	<0.001
air temperature	118 079	1	1204.64	<0.001
cloud cover	13 125	1	133.90	<0.001
rainfall (lag 5 days)	47 841	1	488.07	<0.001
site × air temperature	206 027	3	700.63	<0.001
site × cloud cover	68 784	3	233.91	<0.001
site × rainfall	95 405	3	324.44	<0.001
time × air temperature	8773	3	29.83	<0.001
time × cloud cover	1925	3	6.55	<0.001
time × rainfall	21 040	3	71.55	<0.001
site × time	106 050	9	120.21	<0.001
residuals	5 215 949	53 213		

(c) Relating logger data and microhabitat data

We tested how well variation in temperature and oxygen at the microhabitat level (i.e. spot measurements) can be predicted from measurements in the water column obtained by the logger. For temperature, this yielded strong correlations, which were close to the $y = x$ line (figure 6). This follows from the fact that on any given day, there are no strong temperature gradients, so the logger data with a coarser spatial resolution can accurately reflect the temperatures in the microhabitats. For oxygen saturation, we also found a line close to the $y = x$ line for standing waters, but with much more scatter. In running waters, the variation in microhabitat oxygen saturation could not be explained because loggers showed approximately constant high oxygenation (figure 7). Note that the scatter in oxygen saturation levels in standing waters arises due to differences across microhabitats; when relating oxygen measurements for the microhabitat open water, i.e. near the location at which the loggers were deployed, we observed a strong correlation, so differences in measurement errors across equipment are small (electronic supplementary material, figure S5).

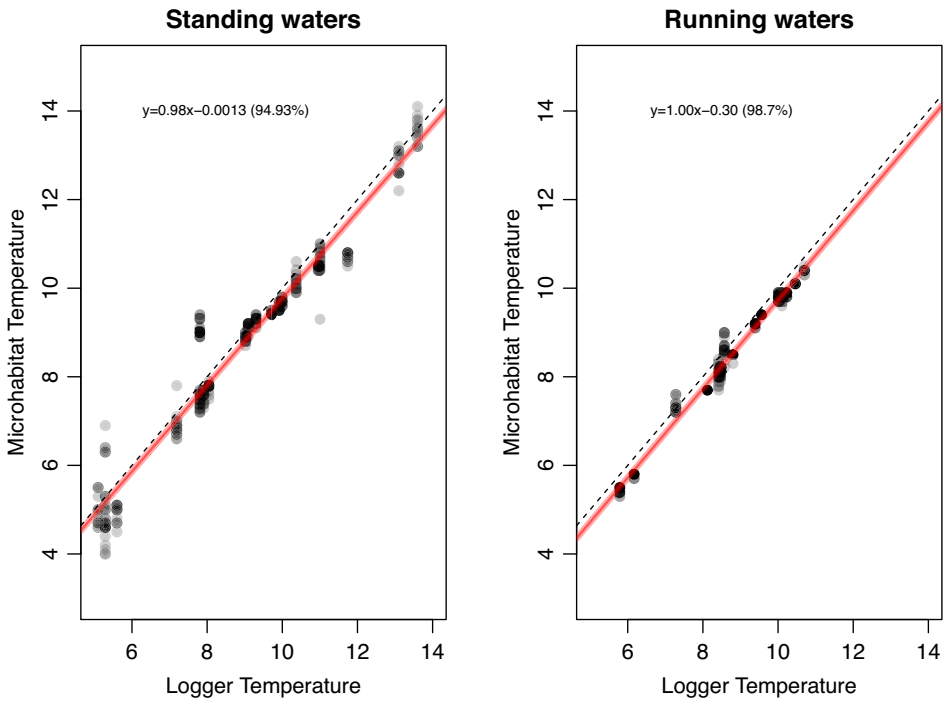

Figure 6. Relationship between the temperature measured by the logger and the temperature measured in microhabitats. Dashed line indicates $y = x$. Red line indicates fitted relationship shown by the equation.

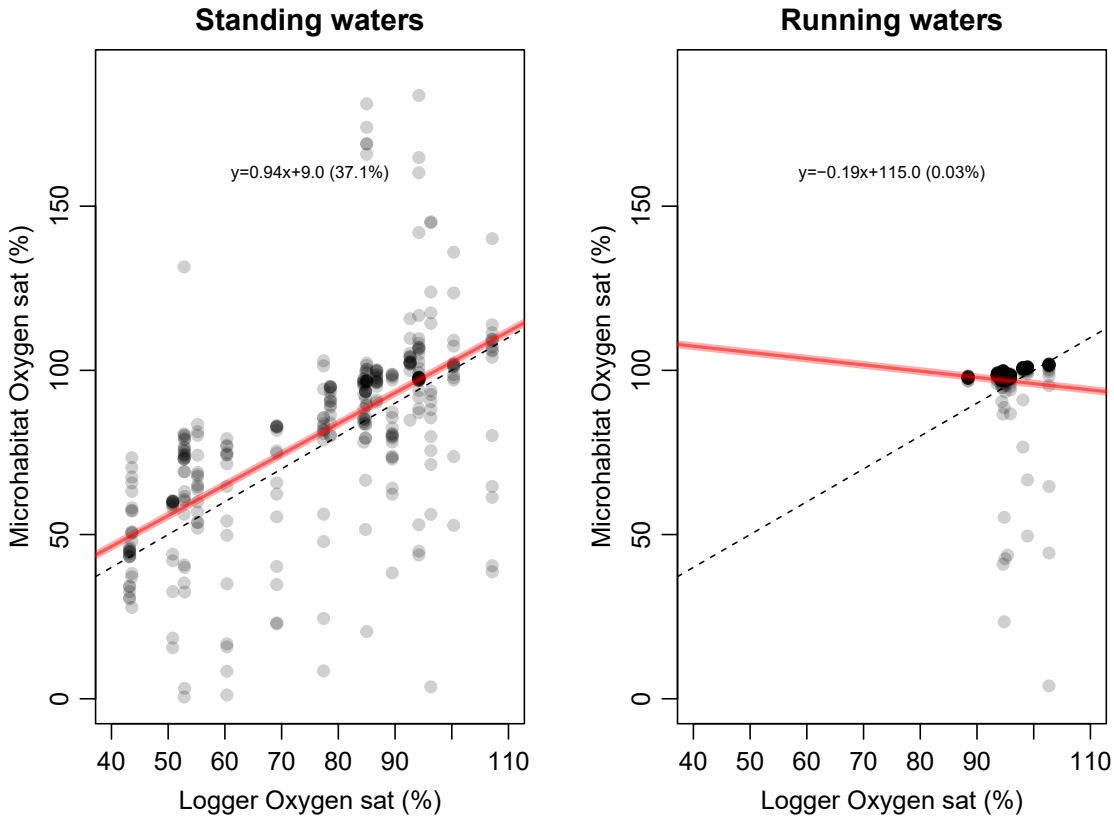

Figure 7. Relationship between oxygen saturation measured by the logger and the temperature measured in microhabitats. Dashed line indicates $y = x$. Red line indicates fitted relationship shown by the equation.

The next step is to further scale up and see how well variation in microhabitat conditions can be related to coarse-resolution weather data. For temperature, variation at the microhabitat scale could be related to coarse-scale weather conditions and time of day (R^2 = 87.1). For oxygen, the variation at the microhabitat scale was weakly associated with coarse-scale weather conditions and time of day (R^2 = 3.7%). Including the site as a factor in these models increased the explained variation

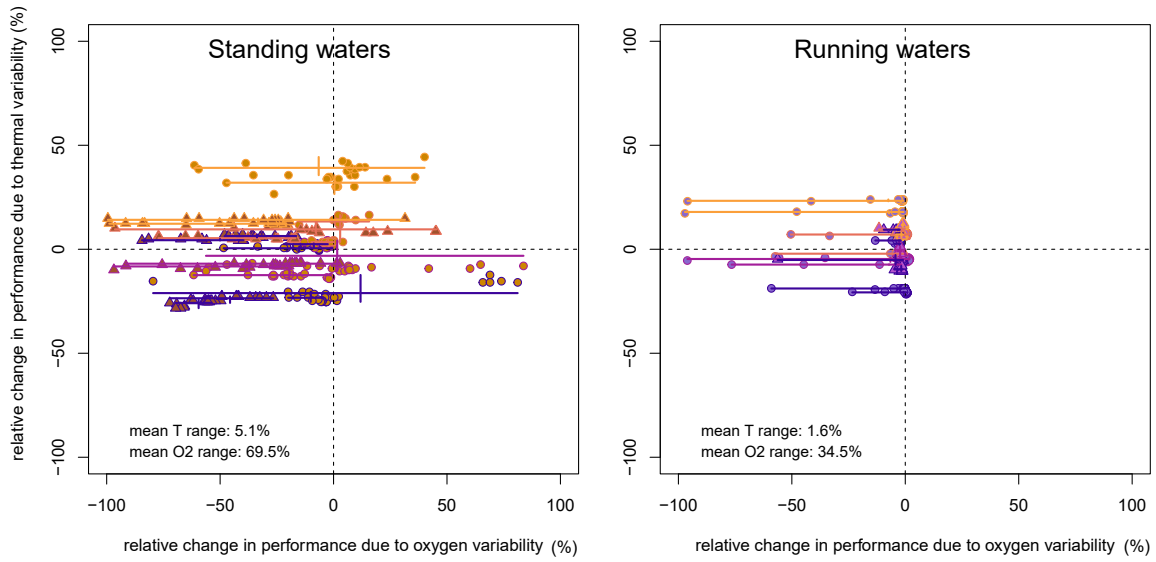

Figure 8. Relative changes in performance due to microhabitat-scale variation in water temperature and oxygenation for standing waters (left panel) and running waters (right panel). See Methods for how variation in temperature and oxygen was translated into performance differences. All spot measurements are shown, and for each sampling day and sampling moment (5 days x 2 sampling times), we calculated the range in performance, shown as vertical (oxygen) and horizontal (temperature) lines.

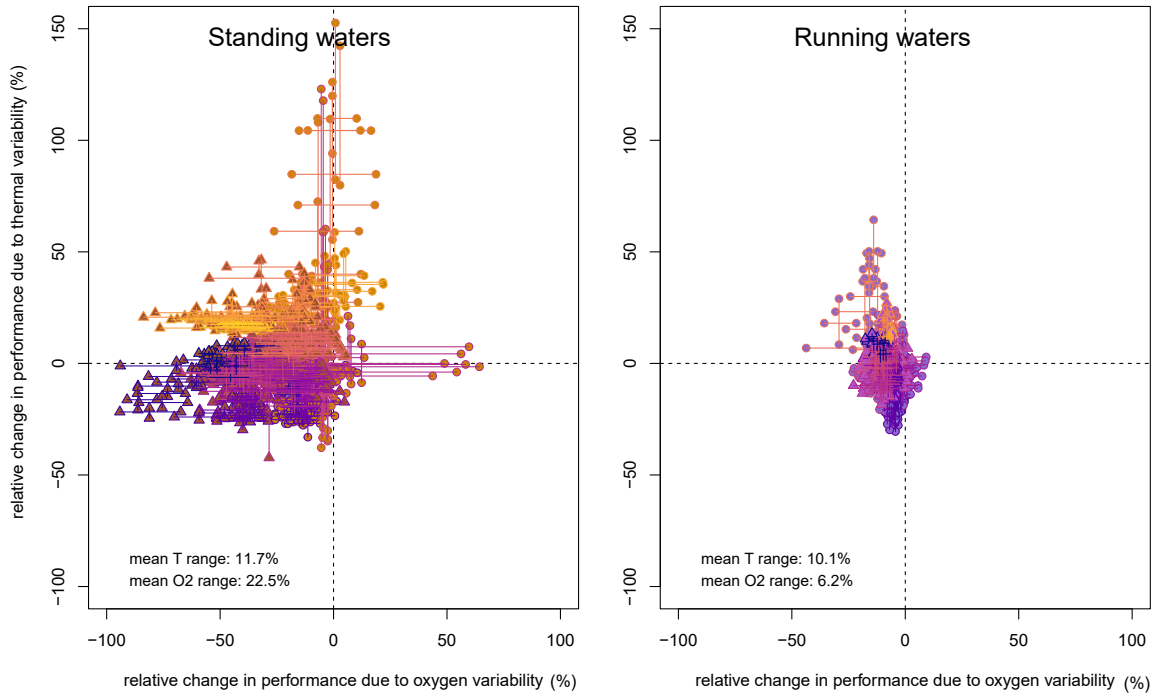

Figure 9. Relative changes in performance due to temporal variation in water temperature and oxygenation for standing waters (left panel) and running waters (right panel). See Methods for how variation in temperature and oxygen was translated into performance differences. All logged data obtained from the water column are shown, and for each sampling day, we calculated the range in performance, shown as vertical (oxygen) and horizontal (temperature) lines.

(temperature: R^2 = 97.9%; oxygen: R^2 = 47.1%). However, site effects here primarily account for unmeasured, site-specific characteristics and therefore lack general predictive power.

(d) Effects of water temperature and oxygenation on performance

Quantifying the conditions that freshwater life is exposed to is, of course, only the first step. By combining exposure with species' sensitivities, we can potentially gauge how it will affect their performance. Although freshwater species differ in their sensitivity to temperature, oxygen and their interaction [4,31,32], we provide a first-order insight by translating the observed variation in water temperature and oxygenation into estimated changes in organismal performance (see Methods). Differences

in performance due to small-scale spatial variation, as captured by the spot measurements in the microhabitat, are primarily due to variation in oxygen (figure 8). At a given measurement moment, differences in performance due to spatial variation in temperature are minor (<6%), whereas differences in oxygen saturation may strongly affect performance (up to 69%), even in running waters (34%).

Temporal differences in performance due to daily fluctuations show a larger effect of temperature (10–12%; figure 9). As oxygen does not fluctuate strongly in the water column in running waters, performance is not much affected (6%), but in the water column of standing waters, oxygen fluctuations have greater effects on organismal performance (23%) than thermal fluctuations (12%).

4. Conclusion

According to Southwood, the habitat is the templet for ecological strategies [8]. Here, we have quantified variation in temperature and oxygen, two key niche axes for aquatic life, something that is rarely done, particularly across biologically relevant spatial scales. Both spatial and diurnal variations in water temperature were minor (in most cases, well below 2°C), at least for the water bodies investigated here, and could be reasonably well predicted from coarser resolution data. In contrast, steep gradients in water oxygenation across small distances (0–15 cm) and over short time periods (daily fluctuations) are the norm in shallow freshwaters. Such gradients were especially pronounced in standing waters, but even in generally well-oxygenated running waters there are pockets of hypoxia.

Running water organisms can, to some extent, escape hypoxic conditions by selecting areas with higher flow [26,27], reducing the boundary layer around their bodies and enhancing oxygen diffusion [33]. However, this likely carries costs in terms of abrasion, predation and dislocation. The fact that oxygen conditions in the microhabitat may be different from water oxygenation measured in the water column may explain why the latter has sometimes been found to be a poor predictor for the occurrence of taxa, such as Ephemeroptera, which was better captured by variation in biochemical oxygen demand (BOD; [27]), as BOD likely better reflects oxygen minima to which stream insects may be exposed in their microhabitats. In standing waters, benthic invertebrates will frequently experience hypoxia in their microhabitats, driving the evolution of strategies to tolerate this, explaining why they are usually fairly resistant to some degree of hypoxia [34]. In conclusion, we show clear contrasts when comparing temperature–oxygen conditions on land and in water, suggesting that animals in water will have much more pronounced adaptations to cope with fluctuations in oxygen [35], while those on land will have evolved adaptations to cope with thermal heterogeneity.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and code used in this manuscript are openly available [36].

Supplementary material is available online.

Declaration of AI use. AI was used to help draft a cover letter.

Authors' contributions. W.C.E.P.V.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; D.T.B.: conceptualization, methodology, project administration, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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