

Opaque closed chambers underestimate methane fluxes of *Phragmites australis* (Cav.) Trin. ex Steud

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Abstract Closed chamber measurements for methane emission estimation are often carried out with opaque chambers to avoid heating of the headspace. However, mainly in wetlands, some plants possess an internal convective gas transport which quickly responds to changes in irradiation. These plants have also been found to often channel a large part of the released methane in temperate fens. We compare methane fluxes derived from transparent versus opaque chambers on *Carex*-, *Phragmites*-, and *Typha*-dominated stands of a temperate fen. Transparent chamber fluxes almost doubled opaque chamber fluxes in the convective transporting *Phragmites* stand. In *Typha*, a trend of higher fluxes determined with the transparent chambers was detectable, whereas in *Carex*, transparent and opaque chamber fluxes did not differ significantly. Thus, opaque chambers bias the outcome of methane measurements, depending on dominant vegetation. We recommend the use of transparent chambers when determining emissions of convective plants or extrapolating fluxes to larger scales.

Keywords Aerenchyma · *Carex* · Convection · Fen · PAR · *Phragmites* · *Typha*

Introduction

Peatlands substantially influence atmospheric concentrations of the three major greenhouse gases (GHGs) carbon dioxide (CO₂), methane, and nitrous oxide (Parish et al. 2008). Due to the growing international recognition of peatlands as GHG sources and sinks (United Nations Framework Convention on Climate Change 2012), reliable estimates of emissions from a wide range of peatland types will be needed in the future.

Commonly, micrometeorological methods (such as eddy covariance) and closed chamber measurements are used to assess GHG emissions. Which technique is preferred depends on multiple factors, since both have assets and drawbacks (Livingston and Hutchinson 1995; Lai 2009; Hendriks et al. 2010). Closed chamber systems are usually chosen for small-scale manipulation experiments or assessments of spatial variability. They are also often employed for methane exchange measurements because the eddy covariance technique is costly, maintenance intensive, and has a number of measurement uncertainties (Lai 2009).

Some wetland plants contribute significantly to the emission of methane by providing a pathway for gases through specialized internal tissues (Wang et al. 1996). These so called aerenchyma tissues mainly serve the transmission of oxygen to the anaerobic root zone. However, simultaneously, they effectively channel methane from the sediment to the atmosphere since they bypass aerobic peat layers in which methane oxidation might occur. As a result, plants transmit up to 90 % of the methane released to the atmosphere from the

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sediment (Morrissey and Livingston 1992; Askaer et al. 2011; Miller 2011). The main driver of gas transmission through the aerenchyma is their diffusion gradient; additionally, some plant species such as *Phragmites*, *Nuphar*, *Typha*, and others are capable of convective transport during daylight hours (Dacey 1981; Armstrong and Armstrong 1991; Bendix et al. 1994). Convective transport in wetland plants often depends on humidity differences between the plant's internal gas spaces and the surrounding air and is therefore susceptible to changes in the plant's microenvironment (Armstrong and Armstrong 1990; Bendix et al. 1994; Arkebauer et al. 2001). At the same time, it responds rapidly to changes in photosynthetically active radiation (PAR), possibly caused by stomata movement (Dacey 1981; Armstrong et al. 1992; Arkebauer et al. 2001). Methane emissions transmitted by such plants immediately decrease with reduced light incidence (Whiting and Chanton 1996; van der Nat and Middelburg 1998, 2000).

In temperate fens, convectively transporting plants are major constituents of the vegetation. Especially, common reed (*Phragmites australis* (CAV.) TRIN. ex STEUD.) dominates large fen areas around the world. This species is also known to have a particular high potential for internal convective flow (Brix et al. 1992; Armstrong et al. 1996). Similarly, the widespread genus *Typha* L. (Cattails) contains several wetland species with high rates of convective flow (Brix et al. 1992; Bendix et al. 1994). In addition, this genus shows diel pressurization patterns resulting in a distinct mid-morning emission peak, after which emissions stay low and are not correlated with PAR (Chanton et al. 1993; Whiting and Chanton 1996). Emission peaks may also be observed in *P. australis* which, however, are more persistent and closely follow PAR (Kozuchowski and Johnson 1978; Kim et al. 1998; Brix et al. 2001). In contrast, plants with only diffusive transport, like many species in the genus *Carex* L. (sedges), show small or no diel emission patterns which are not correlated with PAR (van der Nat et al. 1998; Garnet et al. 2005; Wang and Han 2005). Like the other two species, *Carex* makes up a substantial part of the typical vegetation of temperate fens.

Temperature and relative humidity in the chamber headspace may increase significantly during closed chamber measurements at high irradiances. Therefore, opaque or reflective chambers are commonly preferred for estimating methane and nitrous oxide emissions (e.g. Bastviken et al. 2010; Hendriks et al. 2010; Juszczak and Augustin 2013). Livingston and Hutchinson (1995)

recommend minimization of headspace heating as a precautionary measure against unknown bias. Still, at the same time, they argue that small increases in temperature are rapidly attenuated in the ground and therefore not likely to change the rate of gas exchange between soil and atmosphere. Furthermore, they urge the use of transparent chambers if the physiological functioning of the enclosed plants contributes to the gas exchange process. This is surely the case if the enclosed vegetation is capable of convective transport. Still, due to the long closing times during methane measurements, the use of transparent chambers is problematic. Without temperature control, the abiotic properties of a transparent chamber headspace can change dramatically during chamber placement, which again, may alter the rate of convective transport. Based on investigations of the internal pressurization of *P. australis*, Arkebauer et al. (2001) conclude that chamber measurements over plants with convective throughflow demand particular care regarding, e.g. climate control and light transmission.

Chanton and Whiting (1995) suggest that light-transparent chambers should be used when measuring gas fluxes over any vegetation. However, transparent chambers are utilized only inconsistently throughout the literature, as a result complicating comparisons and meta-analyses. We here assess the effect of the exclusion of light through opaque chambers on methane flux estimates of typical vegetation of temperate fens under field conditions. Based upon the evidence from the literature, we expect lowered flux estimates when using opaque chambers on plants with convective transport.

Materials and methods

We measured methane exchange with one transparent and one opaque closed chamber in the Trebel valley in NE Germany (54°06'N; 12°44'E) in August 2011. The climate is humid but continentally influenced; the mean annual air temperature (data from 1991–2010) is 9.1 °C, and the annual precipitation is 626 mm (data from 1981–2010, German Weather Service). The investigation area is dominated by a minerotrophic percolation mire with peat depths varying from 4 to 6 m. Like most peatlands in this region, it had been heavily drained for intensive agricultural use during the 1960s. In 1997, a 3,000-ha large area including the investigation area was rewetted and dedicated to nature conservation. Since then, hunting constitutes the only land use.

Dominant stands of *Carex acutiformis* EHRH., *P. australis*, and *Typha latifolia* L. were each sampled on three occasions. In each plant stand, we installed two collars 2 weeks prior to the first measurement (insertion depth 10 cm). These were accessible by boardwalk to minimize disturbance during sampling. We used flexible, height-adjustable chambers with an enclosed volume of approximately 0.6 m³. These were manufactured mainly from polyurethane (transparent chamber, light transmissivity >90 %) and thermoplastic polyurethane (opaque chamber).

To avoid headspace heating, we constructed a portable cooling system and connected it to the transparent chamber (Fig. 1). In both chambers (transparent and opaque) headspace, air circulates at the same rate to establish comparable headspace mixing driven by a ventilator installed inside an external pipe. However, at the transparent chamber, parts of the external pipe are enclosed in a Styrofoam box which contains ice-cold water, directly cooling the walls of the pipe. To increase contact surface area, a copper tube helix is installed inside the pipe, through which the surrounding water circulates driven by an electrical pump. The rate of water flow through the copper helix (and by this cooling intensity) is adjustable to avoid cooling of the headspace temperatures below initial conditions. During the measurements, we constantly monitored the temperatures at the inlet of the cooling system and corrected the rate of flow according to the temperature trend.

We measured on 9 days between August 12 and August 29. To account for the high temporal and spatial variability of emissions, we established the following measuring procedure: starting at 06:00 a.m., the transparent and the opaque chambers were simultaneously set up on the two adjacent collars of one plant stand. During the closure time of 40 min, five gas samples were taken using evacuated glass flasks (60 ml). The

chambers were switched following a 20-min lag time, and the measurement was repeated. We continued in this alternating manner until 01:00 p.m., when the last measurement was started. At this time, PPFD had reached its maximum. This procedure resulted in a total of eight measurements on each spot during 1 day (four opaque and four transparent). During the measurements, we also recorded air temperature and relative humidity (RH) inside the chamber with two loggers (Lascar Electronics Ltd., UK) installed at different heights of the chamber wall. Additionally, we documented photosynthetically active photon flux density (PPFD, 400–700 nm) with a quantum sensor (Indium Sensor, Germany) above the plant canopy each time a gas sample was drawn. The gas samples were analyzed for methane and CO₂ concentrations by a gas chromatograph (Perkin Elmer Auto System) with a flame ionization detector (FID) and electron capture detector (ECD) within 24 h.

All statistical analyses were performed using R 2.14.2 (R Development Core Team 2012). We estimated the gas fluxes using the *flux* package (Jurasiński et al. 2012) for R, which fits a number of linear regressions to the data, retaining at least four out of five concentration values and then returns the model with the best fit. Only fluxes with concentrations larger than the minimum repeatable precision of the gas chromatograph and an *R*² of at least 0.8 were included in further analyses. Further, all chamber measurements with temperature changes of more than 5 °C from the start were discarded. The level of significance was 0.05; all the mean values are given with ±1 standard error (SE).

To investigate the specific emission patterns of the vegetation, we sorted the measurements into time classes. Each time class included one measurement each of both chambers on the two adjacent collars, therefore covering one complete experimental cycle. This resulted in a total of four time classes (06:00 to 08:00 a.m., 08:00 to 10:00 a.m., 10:00 a.m. to 12:00 noon, and 12:00 noon to 02:00 p.m.). Because we aimed to assess the impact of the chambers' light transmission on CH₄ fluxes, we then excluded all measurements from the dataset which fell into the first time class to avoid bias by including data gathered under low-light conditions during the early morning. With the remaining values, we calculated linear mixed effect models for each plant stand with chamber type as fixed effect and spot, air temperature, and relative humidity as random effects. For model estimation and *p* value calculation, we used the R packages *lme4* (Bates 2011) and *languageR* (Baayen 2011).

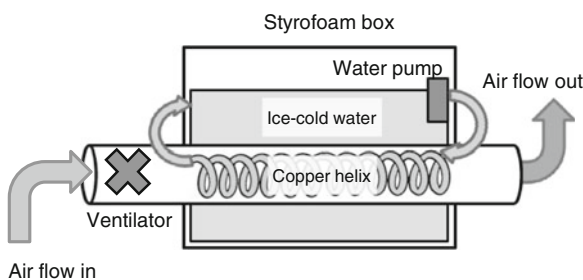


Fig. 1 Illustration of the cooling system connected to the transparent chamber

For comparison of the PPFs between vegetations, we applied pairwise comparisons using Wilcoxon rank sum test with Boniferroni p value adjustment.

Results

From the whole dataset, 12 measurements were excluded because temperature changed more than 5 °C during the closure time. In the remaining measurements ($n=105$), the air temperature increased on average 0.7 ± 0.1 °C in the opaque chamber and 0.4 ± 0.2 °C in the transparent chamber (Fig. 2). The mean relative humidity remained stable in the opaque chamber (0.4 ± 0.4 %) and in the transparent chamber (-0.5 ± 0.7 %).

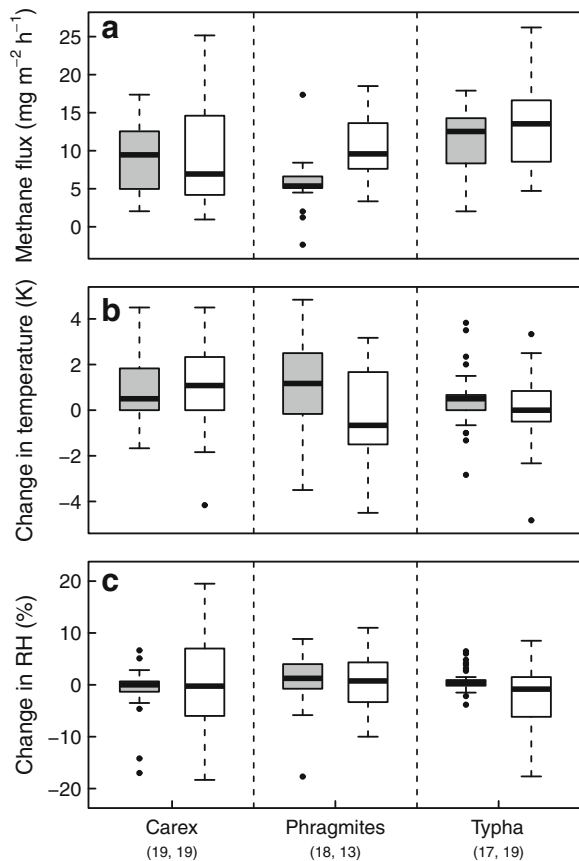


Fig. 2 Methane fluxes (a), changes in air temperature (b), and changes in relative humidity (c) during measurements on three vegetation stands (columns). Grey boxes show opaque chamber data; white boxes show transparent chamber data. The first time class is included in the data. Whiskers mark the data lying within the 1.5 interquartile range. Parentheses below the vegetation names show the number of observations for opaque and transparent chamber measurements, respectively

In the *Phragmites* stand, the mean flux determined with the transparent chamber was more than 1.7-fold when determined using the transparent chamber regardless if the early morning values (06:00 to 08:00) were included or not (Table 1). Contrastingly, in *Carex*, both chamber types did not yield different mean flux estimations. In *Typha*, the fluxes varied slightly between chamber types, with higher fluxes determined with the transparent chamber.

Overall, the chamber effect was highly significant ($p=0.001$) in the *Phragmites* when tested with the linear mixed effect model. The same analysis revealed a trend for higher methane estimates by the transparent chamber in the *Typha* stand ($p=0.07$). In contrast, chamber type was not found to have an effect on estimated fluxes of the diffusive plant stand (*Carex*, $p=0.7$).

Morning emission patterns clearly differed between vegetation types (Fig. 3). In the *Carex* stand, neither opaque nor transparent chamber measurements showed a trend during the morning. In *Phragmites*, the emissions increased during the morning for both chamber types, but the increase was more pronounced for transparent measurements. Transparent chamber measurements in the *Typha* stand varied only slightly during the morning, while opaque measurements decreased from a high initial value.

During our measurements, CO₂ concentrations increased by 22 ± 7 ppm in the opaque chamber. In the transparent chamber, the CO₂ concentrations decreased by 25 ± 13 ppm. Across measurement, the days and time classes mean PPF were 831 ± 34 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the *Carex* stand, 847 ± 29 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the *Phragmites* stand, but significantly lower (619 ± 31 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in the *Typha* stand.

Discussion

Methane emissions were considerably lowered when using opaque chambers on convective plants. In *P. australis*, transparent chamber fluxes were almost doubled (1.7-fold) compared to those of the opaque chamber. Excluding early morning values at low irradiances, *T. latifolia* fluxes determined with the transparent chamber were also higher than those of the opaque chamber. Shading did not have a short-term effect on methane fluxes in the diffusive *Carex* stand in this study. Also, no light-induced emission pattern could be detected during our measurements in this plant stand, as estimates of

Table 1 Mean estimates and SEs of methane fluxes ($\text{mg m}^{-2} \text{h}^{-1}$), together with the comparison of the two chamber types (expressed as the ratio of the mean transparent chamber flux to mean opaque chamber flux). Ratios were set to equal 1 when the SEs of estimates determined with both chamber types overlapped

Vegetation	Including first time class	Mean flux \pm SE (opaque chamber)	Mean flux \pm SE (transparent chamber)	Transparent flux/ opaque flux ratio
<i>Carex</i>	Yes	9.0 \pm 1.1	9.1 \pm 1.5	1
	No	8.5 \pm 1.1	9.0 \pm 1.8	1
<i>Phragmites</i>	Yes	5.6 \pm 0.9	9.9 \pm 1.3	1.8
	No	6.3 \pm 1.0	10.4 \pm 1.3	1.7
<i>Typha</i>	Yes	11.6 \pm 1.0	14.6 \pm 2.0	1.3
	No	10.8 \pm 1.0	14.5 \pm 1.7	1.3

both chamber types across the time classes scattered around one collective mean. These findings are consistent with the present literature concerning diffusive plants (Whiting et al. 1991; Wang and Han 2005; Sun et al. 2013). In the *P. australis* stand, transparent fluxes showed a clear increase from dawn to noon values. The opaque chamber values during the morning also increased at a slower rate. It is possible that plant rhizomes inside the collars were still connected to the surrounding plants and that these partly vented into the opaque chamber through the contained dead culms. Alternatively, the rising emissions might be explainable by increasing soil temperatures during the morning.

P. australis is one of the most widespread and productive plant species in the world (Clevering and Lissner 1999). It is capable of internal pressurization, and the resulting convective air flow drives methane emissions (Chanton et al. 2002). PAR incidence plays a major role in regulating internal pressures and

corresponding methane emissions in *Phragmites* (Armstrong et al. 1992; van der Nat et al. 1998; Arkebauer et al. 2001). Further, methane and carbon dioxide concentrations increase inside the plant's lacunal spaces during periods of darkness (Whiting and Chanton 1996; van der Nat et al. 1998; Chanton et al. 2002). When plants capable of convective transport are shaded, the emissions are therefore delayed until a new steady state in terms of diffusion is established. Following the return of light, the accumulated gases are released at once as an emission peak (van der Nat et al. 1998). This indicates that opaque chamber measurements over convective plants systematically underestimate methane fluxes by stopping the emissions transmitted by plants. Presumably, they do not even accurately represent night-time emissions since the build-up of methane concentration inside the aerenchyma delays the release by diffusion. Hence, the emissions measured by the transparent chamber very likely describe the

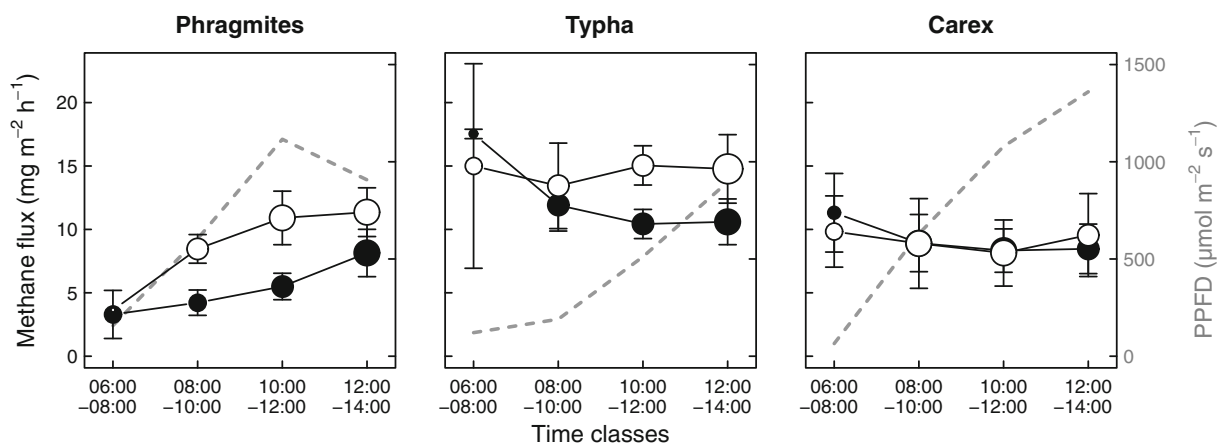


Fig. 3 Emission patterns of methane fluxes estimated with the opaque chamber (black circles) and the transparent chamber (white circles) together with mean PPFDs (dashed line) in different vegetation stands. Circles mark the average value of all

measurements that fall within a given time class; error bars denote standard errors of the mean. The number of observations included in the mean is represented by circle size ($n=1-6$)

actual emissions of convective plants more accurately than those measured with opaque chambers.

Whiting and Chanton (1996) found a reduction in methane emission rates on *Typha* when the (transparent) chambers of their study were shaded. In our study, the difference between transparent and opaque chamber measurements was not significant. Maybe the internal pressures in *Typha* do not react as rapidly as in *Phragmites* to changes in PAR. At the same time, it could be a result of the differing emission patterns which are not closely correlated with PAR in *Typha* (see ‘Introduction’ section). Bendix et al. (1994) were able to relate rapid changes of convection in *T. latifolia* and *T. angustifolia* L. to changes in RH and temperature; however, the influence of light was less pronounced. Using scanning electron microscopy, they located the effective Knudsen pores (a requirement for the build-up of pressure differentials) directly below the leaves' palisade parenchyma. They conclude that (light-induced) stomatal movements therefore do not have a direct effect on convection in this species. However, during the early mornings of our measurement days, the extent of cloud cover differed between vegetations (see Fig. 3). Hence, the significantly lower irradiances during measurements in the *Typha* stand might have masked the chamber effect, leading to statistically indifferent flux values for both chamber types. The opaque chamber values decreased from a high initial value in *Typha*. This mean value was calculated from only three measurements since the other measurements in that time class had to be excluded for not meeting the R^2 requirements. Across vegetations, most fluxes which were eliminated for quality reasons could be found in the first time class. This was mostly because of stepwise increases of the headspace methane concentrations, indicating ebullition events. Consequently, the values of the first time class might have been corrupted by ebullition and should be regarded with caution.

After elimination of some measurements with severe changes in temperature, relative humidity and air temperature in the remaining measurements displayed only slight changes. However, the need for this measure of quality control shows that the cooling system used in this study in some cases reacted too slowly to maintain a constant environment inside the chamber. Convective transport in plants is known to quickly react not only to changes in PAR, but also to changes in air temperature and relative humidity since it is, in most cases, humidity induced (Armstrong and Armstrong 1991; Bendix et al.

1994). Therefore, conditions inside the chamber need to be controlled very carefully to neither increase nor decrease convective flow. CO₂ concentrations changed only slightly during our measurements in the transparent and opaque chambers. Therefore, we do not expect an influence of CO₂-controlled changes of stomatal aperture on our results.

Meanwhile, a growing number of studies have recognized the importance of light-dependent transport mechanisms for methane emissions on convective plants and consequently use transparent chambers (e.g. Dingemans et al. 2011; Ma et al. 2012; de Klein and van der Werf 2013). However, opaque chambers are continuously used in others (e.g. Juutinen et al. 2003; Ström et al. 2007; Tong et al. 2010). Recently, attempts have been made to describe the global methane budgets through process-based models in order to avoid magnification of measurement errors during extrapolation of ground-based measurements (Wania et al. 2010; Meng et al. 2012; Schuldt et al. 2013). However, methane emissions are most directly controlled by local conditions which are only poorly represented by global models (Ortiz-Llorente and Alvarez-Cobelas 2012). Therefore, bottom-up approaches like closed chamber measurements are essential for model evaluation and investigation of local emission regimes. If such reference measurements are corrupted, model outputs may be biased to an unknown extent. In order to yield precise results during chamber measurements, it is vital to be well aware of the composition of the contained vegetation and to adapt the measurement routine to the prevailing gas transport mechanisms. This might include adjustments of the chamber light transmission, as well as adaptations of measurement times (relative to emission peaks).

Rapid responses of reduced light have also been shown for convective *Nuphar lutea* (L.) SIBTH. & SM. (Dacey 1981) and are likely to apply also to other convective plant species (Chanton and Whiting 1995). Also, such light effects have been documented for many different climatic zones (Brix et al. 1992; Arkebauer et al. 2001) and should therefore not be limited to the temperate zone.

Conclusions

Opaque chambers very likely underestimate methane fluxes on plants with convective internal transport. In

our opinion, if the vegetation is capable of convective transport, there is no alternative to the use of transparent chambers. This holds especially if the data are used to extrapolate emission values to large temporal and spatial scales because the error scales with the areal extent. If transparent chamber measurement should constitute the standard for methane emission analysis in the future, sensitive portable cooling systems need to be developed. For meta-analyses, it is vital to account for different levels of light transmission of chambers on plants with convective transport. To further quantify the impact of opaque chambers, future studies should compare long-term data of both chamber types with eddy covariance measurements, or directly measure internal pressures and methane concentrations in the aerenchyma during chamber placement.

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Conflict of interest The authors declare that they have no conflict of interest.

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