Dear Paul Stoy et al.

your revised manuscript "Methane efflux from an American bison herd" has been seen by two independent reviewers. Both reviewers think that the study is innovative, interesting and valuable despite the relatively short time period of observations.
Yet, both reviewers are also critical, with reviewer 1 questioning the approach taken to assess spatial uncertainty and reviewer 2 being particularly critical about the use of the two footprint models and the assumption on where methane is emitted from ie difference in height between snow surface vs bison head resulting in a major revisions suggestion. Given the additional comments made, the paper is not yet ready for publication.
While this is the second round of reviews, both reviewers as well as myself share the opinion of this being a valuable study, Thus, I ask you to address the issues raised by clarifying and possible simplifying the manuscript as well as by removing the speculative bits.

with kind regards

Lutz Merbold
Referee #3

We thank the Referees for their insightful comments. They raise a number of important technical points, many of which were particularly welcome because they helped simplify the analysis. We detail our responses to each point below. Thank you for your continued support of this manuscript and we hope that we have addressed the Referees' comments adequately.

Review of manuscript bg-2020-38-manuscript-version4

This is my first review of an already revised manuscript by Stoy et al. The authors present about 2.5 months of EC flux measurements for methane over a snow-covered pasture field with a managed bison herd. By combining the camera image derived distribution of the animals with EC footprint models the average daily emission rate per animal was derived. The study adopts methods already presented in previous studies (Felber et al., 2015; Dumortier et al., 2017; 2019) with the new element of using camera images to visually determine the position of the animals on the pasture field.

Since, according to the authors, the study presents the first actual measurement of CH4 emissions by bison, the results are valuable despite the limited time period.
However, the manuscript presently suffers from a number of issues that need major revisions before the manuscript is suitable for publication. They are listed in the following comments.

Thank you for your insight, you have raised a number of points that have been on our mind. We hope that we have adequately addressed these in the responses below.

MAJOR COMMENTS

1) line 24-25 (and throughout manuscript): I find it generally useful to apply two different footprint models in such a study. However, the animal emission results obtained with the two

models should not be treated separately throughout the manuscript and in the abstract. This is not very useful (or even confusing) for the reader, unless the authors want to focus on the specific model differences in detail (which is in my understanding not the scope of this study). Instead, the authors should treat the difference induced by the two models as a part of the footprint model uncertainty. Thus, they should either take the average result of the two models as best guess or declare the preference of one of the models and use only that for the final results.

We agree with this comment; we added both footprint models in response to previous reviews and agree that continually noting them both is excessive. Instead we take your advice to focus on the average of both and to use their differences to gain insight into uncertainties due to choice of footprint model. We retain many of the figures that detail the different behavior of the models as we feel that it helps provide clarity as to why they are different.

2) line 138-139: This statement is too optimistic. Heidbach et al. (2017) found considerable differences between different footprint models. For a feedlot experiment, Prajapati and Santos (2018) also found large differences in the spatial extension of footprint models (as mentioned later in lines 326ff.). Therefore, the (systematic) uncertainty effect of the footprint calculation seems to be underestimated in this study (see also comments 3 and 5), although the authors claim a conservative uncertainty estimation.

Footprint model accuracy is an ongoing challenge in flux science. The purpose of this experiment is not to compare footprint models given that measurements were made under field conditions at a working ranch with non-domesticated animals rather than an experimentally controlled setting. Rather than add additional footprint models, we revised the language of the manuscript to note that uncertainties due to footprint modeling may be larger than we estimate using the two models chosen here. We then further emphasize that robust approaches to estimating footprint uncertainty remain a critical area of future research.

3) line 146-147: The calculation and use of individual ("unique") z_0 values for each half hour is problematic in my view. Such z_0 values can vary a lot (even if the roughness conditions in the footprint remains unchanged) especially at low wind speeds. I would therefore like to see the obtained roughness length values in this study and eventually recommend to constrain them to a plausible range. Otherwise, the uncertainty of the footprints may be much larger than expected.

The effect of grazing animals in the flux footprint on the effective roughness length z_0 has been analysed e.g. by Felber et al. (2015). It would be useful to compare those results with the findings in the present study.

We somewhat disagree with this comment because we feel that animal movement results in a situation where z_0 is dynamic across time. The approach of Felber et al. (2015) for constraining the likely range of z_0 is interesting and they are correct in noting that it should take a reasonably constrained seasonal course as a function of grass height in their case. In our conditions with snow and obstacles (animals), we argue that it makes sense to consider z_0 as a dynamic variable because it can change rapidly. We did in retrospect take elements of the approach of Felber et al. (2015) by thresholding the extreme values that result when the denominator of the equation for z_0 approach zero. This thresholding only impacted 15 of 3117 observations.

4) line 160-170: The concept description of the footprint approach is not fully appropriate and unnecessarily complicated.

a) Eq. 4 is in fact the generic definition (in a discretized math. form) of the footprint weight function ϕ_{ij} as presented e.g. by Schmid (1997). It is valid for all EC measurements.

This is correct. We are starting with the basics. This equation was also presented by Dumortier et al. (2019) as noted and we adjusted it for the dimensions of our field. We added the Schmid (1997) reference for completeness.

b) Eq. 5 is unnecessary and complicates the concept presentation. It would be much better to introduce here the (simplifying) assumption of equal average flux per bison $\langle f_{ij} \rangle$ in the following way: $F_{ij} = n_{ij} \langle f_{ij} \rangle$.
Inserted in Eq. 4 this directly leads to Eq. 6.

We understand what you are saying but we do not feel that equation 5 is unnecessary because it is rather simple and defines f_X, used in the next equation. It is taken from Dumortier et al. (2019) as indicated, which was the inspiration for the footprint approach, where it also happens to be their equation 5. We note also in response to Referee #4 that we did erroneously list the normalization term $\Delta x_{ij} \Delta y_{ij}$ twice in equations 4 and 6. This has been corrected in the revised manuscript and did not impact the results.

5) line 214-215: Obviously the methane emission by the bison was assumed to be a ground source in the footprint models (i.e. the snow surface in the present experiment). This is clearly questionable since the mouth/nose of a bison (main source) is not generally at ground level. I would assume an average height of 30 to 50 cm. In addition, the exhaled air has an upward inertia due to its high temperature (especially in winter) that leads to an even higher effective source height for the model. It needs to be discussed (or tested) what error/uncertainty is introduced by a wrong emission height.

This is a topic that we discussed when preparing the paper. As it happens, measured snow depth was nearly 30 cm across much of the measurement period, noting that snow depth across the entire field becomes rather dynamic due to drifting and trampling. Per the latter point, when bison are grazing, which is often, their mouths are *underneath* the snow surface. We agree that a brief discussion of methane release heights is warranted and have added it to the text, but we have little basis to adjust release height up and down for the dynamic vertical head movements of multiple animals so we did not pursue this as we felt that it would add uncertainty.

The second point regarding temperature differences also came to mind when designing the experiment. Methane leaves the animal at its body temperature, which almost always differs from air temperature. Heat is also transferred more efficiently than passive scalars in the convective sublayer (e.g. Katul et al., 1995, DOI: 10.1007/BF00712120) so we cannot assume that methane is equally buoyant to heat. This brings to mind the need to explore heated point release experiments and footprint models to quantify the importance of heated air parcels in biogeochemical studies, and we now note both of these topics in the revised Discussion section.

6) line 260ff. The discussion of the obtained results in comparison to existing literature information is unsystematic and clearly insufficient. The methane emission of bovine animals mainly depends on the amount of feed intake and its (digestible) energy content (see line 64- 65). The feed intake depends on the energy demand of the animal, which is itself a function of the body weight and the productivity (milk yield, weight gain). This has to be taken into account when discussing the different CH4 emissions by different animals in other studies.
It could be checked whether existing functional relationships for bovine animals (depending on animal weight and feed amount and characteristics, as given in Table S1-S3) could be used to calculate emissions for comparison with the EC derived results.
The authors cited Kelliher and Clark (2010), Smith et al. (2016) and Hristov (2012) in the introduction (line 59-63) to point out the importance of bison CH4 emission in pre-industrial times. These authors obviously use estimates of typical bison CH4 emissions. Why are those results not included in the discussion in comparison to the results of the present study.

Previous studies noted a rather wide range of methane emission results from different animals as a function of food quality and quantity. Methane flux is related to the animal in question, its body mass, diet, metabolic state, pregnancy / weaning status, and more. Any universal model for methane flux – and we are aware of none – must account for all of these variables.

It would be interesting to create such a model, but this exceeds the scope of the present study. We did check to see if the different nutrient content of the different hay bails (Table S2) impacted methane flux and found evidence that they did at the $P < 0.1$ level but not the more commonly used $P < 0.05$. We did not subsequently dwell on this result because we were not interested in reporting results of questionable significance. In lieu of a comprehensive analysis of all previously published methane flux results, which would be an interesting topic for a review paper, we noted results that are similar to ours. This required a bit of digging; the comparisons to both the Hammond et al. (2016) results and the Prajapati and Santos (2019) results came from a careful analysis of their tables and figures. The purpose of the comparisons is to note that our results have a foundation in the literature.

The Kelliher and Clark (2010) used the Galbraith et al. (1998) penned bison flux estimates and adjusted them for metabolic scalars determined for cattle. The Smith et al. (2016) manuscript uses the Kelliher and Clark estimates, and Hristov (2012) uses a combination of both. Because we questioned the extrapolation of methane flux measurements in a penned animal fed pelletized feed to conditions in the field, we likewise did not belabor a comparison in the Discussion section but rather applaud the efforts of all of the authors for making these difficult measurements and applying them for an improved understanding of the earth system.

7) line 281-309: This section has a misleading title because it only discusses fluxes with bison absent from the pasture field. I also consider this part as quite speculative because it is based on a small dataset. Given that the soil/surface methane fluxes are negligible in comparison to the animal enteric fermentation emissions (Fig. 8), this section is not contributing significantly to the aims of the study and should be shortened drastically or should be fully omitted. In turn, the discussion of entheric CH4 emission needs to be expanded (see previous comment).

We wanted to take care to ensure that methane efflux can be attributed to bison and not other factors in a pasture near a river. We still have hundreds of measurements even though the data record is not as long as some other flux studies. It would have been nice to have a longer data record but we did not wish to alter the bison management strategy of the landowner; the animals were moved to a different pasture at the end of their tenure in the field that we instrumented. We did not leave instrumentation on the field for an extended period after the bison left in order to avoid unnecessary conflict with the landowner. We agree that the title of the subsection could be more accurate and we now write: '4.1 Methane and carbon dioxide efflux in response to environmental variables and bison presence'.

8) Figure 3: This graph is not useful to provide a (quantitative) information of a typical flux footprint extension. It should be changed to a contour plot with contour lines enclosing areas of 50%, 70%, 90% contribution to the flux (as commonly provided in similar studies).
Also the u* and z/L values of the displayed example should be indicated in the figure caption.

We created a figure that exhibits both the Hsieh et al. (2000) and Kljun et al. (2015) footprints for a single half-hourly measurement period, thank you for the suggestion.

9) It would be useful to add a (short) specific Conclusions section

We deliberated this but we summarized findings in the first paragraph of the Discussion and any conclusion would be somewhat redundant with the Abstract. We omitted a Conclusions section for brevity noting that the end of the Discussion section expands the text back to the earth system processes that motivated the original study.

MINOR COMMENTS

line 25: "...similar to eddy covariance measurements of methane efflux from a cattle feedlot during winter". This is a very unclear statement. I suggest to clarify e.g. to: "...similar to previously reported eddy covariance derived cattle methane emissions in a feedlot during winter".

We have to disagree with this point. We feel that the text as written is more efficient and equally if not more accurate because methane emissions in this case will arise from more than cattle themselves; manure will also be a methane source in a feedlot system even if it might be relatively minor depending on how it is managed.

line 47-49: The message of this sentence is misleading. When comparing bison to other ruminants in agricultural production, the differences in productivity (rate of weight increase) and the general energy demand of the animal is much more important for the CH_4 emission than some grazing preference details.

We also have to disagree with this point because multiple studies have demonstrated the importance of diet and herd management for ruminant methane emissions, for example Waghorn et al. (2011, 10.1016/j.anifeedsci.2011.04.019). We agree in general that productivity and energy demand are critical for methane efflux but extensive effort is underway to change ruminant feed to minimize methane losses, which demonstrates the importance of feed.

line 52-55: It appears not logical that the authors first cite studies from 2013 and 2017 and afterwards state "Recent studies have revised methane emission estimates from livestock upward by over 10%" with citing of mainly older (!) studies. Please rephrase.

Measurements were made in 2017 and 2018 so the 2017 reference was quite new at the time and the 2013 reference was not exactly older. We revised the statement to read 'Methane emission estimates from livestock have tended to increase as more information becomes available'.

line 185: "perfectly aggregated" sounds strange in this context (because the animals need to be distant to each other, i.e. non-aggregated). I suggest to change to "perfectly distributed".

We agree that the suggestion makes the text more clear and changed it.

line 188: "...the true number of each bison..." is unclear. Moreover, what is the difference between the true number and the measured number? Please rephrase and clarify.

All measurements have uncertainty. We reworded the text to state 'All observations have uncertainty so estimates of bison location using cameras provides an initial guess of the true location.' In the revised manuscript we now use camera observations as an initial guess of the bison location and add a stochastic uncertainty analysis.

line 324-329: This is a quite unspecific discussion of the problem without a clear conclusion concerning the effect of footprint uncertainty (see comment 2 above).

We do not feel that the issue of footprint uncertainty has been adequately addressed by the community; adding more footprint models will likely lead to more uncertainty

line 338-340: It should be mentioned here, that eddy covariance might not be suitable to determine (separate) the efflux of individual animals on the pasture even if they can be identified and tracked (especially because they tend to move in groups).

This is an interesting point and we agree. We added 'That being said it will be difficult to measure the methane contributions of individual animals in species that tend to herd using eddy covariance'.

Figure 7 caption: Change to "...from the study pasture near Gallatin Gateway ..."

We like this suggestion and have changed the text.

ADDITIONAL REFERENCES

Prajapati, P., and E.A. Santos. 2018. Estimating methane emissions from beef cattle in a feedlot using the eddy covariance technique and footprint analysis. Agric. For. Meteorol. 258:18–28. doi:10.1016/j.agrformet.2017.08.004

Schmid, H.P. 1997. Experimental design for flux measurements: matching scales of observations and fluxes. Agric. For. Meteorol., 87, 179–200.

Referee #4

I really appreciate the reading of this paper which is well written. The application of eddy covariance to wild animals is innovative and interesting. The method is well described and the obtained results are very clear. However, I have the following major remarks:

I do not see the point of using the Tikhonov Regularization method. If cattle location were biased, their location could more or less aggregated than observed. Moreover, cattle could be present in a pixel different than the one expected. I do not understand why the spatial uncertainty should be estimated by smoothing cattle distribution. In my opinion, a better way to estimate spatial uncertainty would be to consider that some part of the herd might not be in the expected cell but in an adjacent cell, even if it results in a more aggregated cattle distribution (e.g. 10% of the herd is considered as mislocated in a specific direction, one iteration could be done for each cardinal direction). As this element represent an important part of the manuscript I suggest either to better explain why the proposed option is the good one (which I am not convinced) or to propose another spatial uncertainty estimation method.

Thank you for the kind comments and insightful review. In an earlier version of the manuscript we included a table that presented average per-bison methane flux estimates after shifting their locations relative to the footprint in the four cardinal directions. Previous referees deemed this unpalatable so we did away with it.

We chose the Tikhonov Regularization method as a sensitivity analysis in part because it does its effects can be visualized on a single axis and it not include a stochastic component that would require Monte Carlo methods. We agree with you that it would be interesting to explore other methods and this comment made us rethink the best way of exploring uncertainty due to spatial location.

A random distribution of locations across space follows a Poisson point process. But our pictures reveal more about bison locations than a random draw. Instead, we now use the bison observations as an initial guess, use Tikhonov Regularization to simulate likelihood surfaces, and then simulate a distribution of bison that uses observations as a prior but adds a stochastic component to bison movement within half-hour periods. We feel that maintaining the Tikhonov Regularization is important to give a finite likelihood for the Poisson point process to allocate bison to pixels adjacent to where they were estimated. We now present the original sensitivity analysis Tikhonov Regularization in a new Supplemental Information section.

There is a problem with Equation 6 which should be written as:

$$\langle f_x \rangle = F_x / \left(\sum_{i=1}^{8} \sum_{j=1}^{12} n_{ij} \phi_{ij} \right)$$

f_x corresponds to mol animal-1 s-1

F_x corresponds to mol m-2 s-1
n_ij corresponds to an amount of animals
ϕ_ij corresponds to m-2
The equation proposed in the manuscript is not homogeneous. I hope that the equation which was applied in the calculations was the one described here above and not the one described in the manuscript.

Thank you for noticing this, we accidentally wrote the scaling factor Δx_ij Δy_ij twice in both equations 4 and 6 in the text but not in the code used for the calculations. We corrected the text.

I also have the following minor remarks:
-line 27 to 28: wording: "Our observations point to the need for direct comparisons of methane emissions from conventional and alternate grazing systems using eddy covariance": I do not see the link between observations and grazing management.

Bison grazing typically replaces cattle grazing systems in rangelands. We re-worded the last sentence of the abstract in response to this and other comments.

-line 43: wording: "also need not migrat
-line 44: The fact that bison do not follow the "green wave" and that they tend to stimulate plant growth does not suggest that they select for forage quality rather than quantity.

We understand how this was confusing on lines 43-44; stimulating plant growth implies that nutrient-rich young leaves are being eaten but this is indirect. Instead we simplified the text to read: They tend to graze in preferred meadows during winter and search broadly for the most energy-dense forages during the growing season (Fortin et al., 2003 Geremia et al., 2019), often in areas which have recently burned (Allred et al., 1991; Coppedge and Shaw, 1998; Vinton et al., 1993).

-line 86 / Table S3: the average mass of a bail should be specified.

Thank you for pointing this out, we have added average bail mass to the table legend.

-Equation 2 /3: is it an "α" (Equation 2) or a "a" (Equation 3).

The equation should have *a* because α is used in Equation 7. Thank you for noticing this error.

-line 159:I would say: "are solely due to"

We feel that 'solely' is probably too strong a word as there are certainly minor sources and sinks distributed throughout the field that average to approximately zero.

-line 216: Giving the mean and median wind direction is of limited interest (e.i. if there are 2 main wind directions, the mean wind direction will be in-between, in a direction from which the wind might never be coming from). Main wind directions are far more relevant.

We agree in principle and the previous version of the manuscript included a histogram of wind directions. Because the wind rose shows a predominant wind direction (Figure 6) we feel that discussing the mean is accurate in our case.

-line 243: Wording: I would say 'At least one bison was located within…"
-line 244: which
-line 244 to 245: wording: "an average of 8 models which increased to both footprint models"?

We revised the wording in these passages and also revised wording throughout the manuscript for clarity when we felt it necessary.

-line 265-278: In my opinion, the discussion would be more interesting if emission comparisons would consider animal body weight => e.g. comparisons in 〖kg〗 _CH4 〖kg〗 _bw^(-1) 〖day〗 ^(-1)

We hesitated to perform this analysis because of how the animals tended to cluster with younger animals often nearer larger animals and larger animals often roaming more throughout the pasture, i.e. smaller animals were infrequently alone. Our approach did not allow us to track animals individually but we agree with the comment that it would be interesting to perform such an analysis if it could be done without introducing potential biases.

-line 301: Gourlez de la Motte

Thank you for instructing us on the correct usage here and on line 311 below.

-line 303: Results from Dengel indicate that CH_4 fluxes are more important during summer but the main reason is a higher stocking density on the pasture. Manure impact on this result is expected to be weak / negligible as manure is not placed in anaerobic conditions. I do not think that the publication from Dengel support the associated sentence.

We revised the sentence to note that manure may be a methane source but is likely rather low in rangeland systems for which we now cite Steed Jr. and Hashimoto (1994).

-line 311: Gourlez de la Motte

(see above)

-line 345 : wording : « algorithms for are »

We corrected the passage, thank you for noticing this.

-line 351: remove "and"

We carefully read the passage and are not sure what this note refers to, but we should note that we comprehensively reviewed the manuscript for minor usage errors.

-Figure 11: the second “Figure 11” should be named “Figure 12”.

This is correct, we made a clerical error when rearranging figures. The figure legends and their references in the text are now corrected.

Methane efflux from an American bison herd

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Abstract. American bison (*Bison bison* L.) have recovered from the brink of extinction over the past century. Bison reintroduction creates multiple environmental benefits but impacts on greenhouse gas emissions are poorly understood. Bison are thought to have produced some 2 Tg year^{-1} of the estimated 9-15 Tg year^{-1} of pre-industrial enteric methane emissions, but few measurements have been made due to their mobile grazing habits and safety issues. Here, we measure methane and carbon dioxide fluxes from a bison herd on an enclosed pasture during daytime periods in winter using eddy covariance. Methane emissions from the study area were negligible in the absence of bison (mean ± standard deviation = −0.0009 ± 0.008 µmol m^{-2} s^{-1} µmol m^{-2} s^{-1}) and were significantly greater than zero, 0.048 ± 0.082 µmol m^{-2} s^{-1}, with a positively skewed distribution, when bison were present. We coupled bison location estimates from automated camera images with two independent flux footprint models to calculate an average (± standard deviation) per-animal methane efflux of 58.5 ± 8.3 µmol s^{-1} bison^{-1}, or 81 ± 11.5 g CH_4 bison^{-1} day^{-1}, similar to eddy covariance measurements of methane efflux from a cattle feedlot during winter. Uncertainties were dominated by bison location estimates (50% of the total uncertainty), then the flux footprint model (36%) and the eddy covariance measurements (14%) suggesting that higher-resolution animal location estimates is a logical starting point for decreasing uncertainty. Annual measurements are ultimately necessary to determine the full greenhouse gas burden of bison grazing systems. Our observations highlight the need to compare greenhouse gas emissions from different ruminant grazing systems and demonstrate the potential for using eddy covariance to measure methane efflux from non-domesticated animals.

1 Introduction

The American bison (*Bison bison* L.) was hunted to near extinction during European expansion across North America (Flores 1991, Isenberg 2000, Smits 1995). Fewer than 100 reproductive individuals existed on private ranches in the United States during the late 19th Century from an original population of 30 – 60 million (Hedrick, 2009). The current bison population of about 500,000 is due to the collective efforts of sovereign Indian tribes, government agencies, and private landowners (Gates

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- **Deleted:** on a per-animal basis, which varied from 55
- **Deleted:** to 62 µmol s^{-1} bison^{-1}. Per-animal methane efflux estimates were also sensitive to uncertainties in bison location, and sensitivity analyses suggest that a conservative uncertainty estimate is on the order of 22%. Combined with conservative uncertainty estimates of the eddy covariance measurements themselves, we arrive at methane flux estimates of 76 ± 21
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et al., 2010; Sanderson et al., 2008; Zontek, 2007), all of whom have spurred a growing interest in bison reintroduction. The bison population is likely to further increase, increasing the incentive for researchers and land managers to understand the environmental impacts of their expansion.

The ecological role of bison has become better understood as populations have recovered (Allred et al., 2001; Hanson 1994; Knapp et al., 1999). Bison feed preferentially on grasses (Plumb and Dodd, 1993; Steuter and Hidinger, 1999) and enhance forb diversity as a result (Collins, 1998; Hartnett et al., 1996, Towne et al., 2005). They tend to graze in preferred meadows during winter and search broadly for the most energy-dense forages during the growing season (Fortin et al., 2003 Geremia et al., 2019), often in areas which have recently burned (Allred et al., 1991; Coppedge and Shaw, 1998; Vinton et al., 1993). Combined, these observations suggest that bison select for forage quality rather than quantity which likely impacts their efflux of methane – which all ruminants emit – because ruminant methane emission is related to feed quality (Hammond et al., 2016) including cellulose and hemicellulose intake (Moe and Tyrrell, 1979). It remains unclear how much methane results from the cellulose-rich grass-dominated diet of bison given their preference for fresh foliage, and if management for bison may increase or diminish the greenhouse gas burden of ruminant-based agriculture.

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Atmospheric methane concentrations have been rising at an accelerated rate since 2016 for reasons that remain unclear (Nisbet et al., 2019) and there is an urgent need to improve our understanding of its surface-atmosphere flux. Between 30 and 40 percent of current anthropogenic methane emissions are due to enteric fermentation in livestock (Kirschke et al., 2013) and the greenhouse gas burden of cattle alone is some 5 Pg of carbon dioxide equivalent per year (Gerber et al., 2013; FAO, 2017). Methane emission estimates from livestock have tended to increase as more information becomes available (Beauchemin et al., 2008; Thornton and Herrero, 2010; Wolf et al., 2017), further emphasizing their critical role in global greenhouse gas budgets (Reisinger and Clark, 2017). Reducing unnecessary greenhouse gas emissions is a global imperative for Earth system management and reducing enteric methane sources is seen as a promising approach to do so (Boadi et al., 2002; DeRamus et al., 2003; Herrero, et al., 2016; Hristov et al., 2013; Johnson and Johnson, 1995; Moss et al., 2000).

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Bison in North America are thought to have been responsible for some 2.2 Tg year^{-1} (Kelliher and Clark, 2010; Smith et al., 2016) of the 9-15 Tg year^{-1} of pre-industrial enteric methane emissions (Thompson et al., 1993; Chappellaz et al., 1993; Subak, 1994). Enteric CH_4 emissions from wild ruminants in the United States in the pre-settlement period comprised nearly 90% of current CH_4 emissions from domesticated ruminants assuming an historic bison population size of 50 million (Hristov, 2012), further demonstrating the importance of bison to methane fluxes in the past. The current and future contribution of non-domesticated ungulates to methane fluxes are uncertain (Crutzen et al., 1985). Previous approaches used inventory approaches or scaling equations that were not derived using methane efflux measurements from bison; the only direct bison methane flux observations that we are aware of measured 30 L per kg dry food intake (17 g methane per kg dry food intake) in one-year-old penned female bison fed alfalfa pellets (Galbraith et al., 1998), more than elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) on a dry matter intake basis and similar to dairy cattle fed high maize silage (Hammond et al., 2016). Cattle methane emissions tend to be greater when fed alfalfa than grass (Chaves et al., 2006) such that existing published values may not represent an accurate estimate of the methane efflux from bison in a natural field setting, which has not been measured to date.

Here, we measure methane flux from a bison herd on winter pasture using the eddy covariance technique (Dengel et al., 2011; Felber et al., 2015; Prajapati and Santos, 2018; Sun et al., 2015). We use flux footprint analyses combined with bison locations determined using automated cameras to estimate methane flux on a per-animal basis and discuss observations in the context of eddy covariance methane flux measurements from other ruminants.

2 Methods

2.1 Study site

The study site is a 5.5-hectare pasture on the Flying D Ranch near Gallatin Gateway, Montana, USA (45.557, −111.229) on a floodplain immediately west of the Gallatin River (Figure 1). Daily high temperatures average 1.6 °C and daily low temperatures average −11.5 °C at Bozeman Yellowstone International Airport (BZN), located 24 km north-northeast of the site, during the November – February measurement period. BZN records an average of 18.2 mm of precipitation per month during November – February, almost entirely as snowfall. A herd of 39 bison entered the pasture on November 17, 2017 and left on February 3, 2018. The mean (standard error) bison weight measured by the landowners on November 16, 2017 before bison entered the pasture was 329 ± 28 kg and the bison varied in age from 0.5 to 7.5 years old (Table S1). Bison consumed a mixture of perennial grasses grown *in situ* that was supplemented by perennial grass hay grown in nearby fields (Table S2) delivered every three days on average (Table S3).

2.2 Instrumentation

A 3-m tower was installed near the center of the study pasture during November 2017 (Figure 1) and surrounded by electric fencing to avoid bison damage. Four game cameras (TimelapseCam, Wingscapes, EBSCO Industries, Inc., Birmingham, AL, USA) were mounted to the tower and pointed in cardinal directions. Two additional game cameras were mounted near the pasture edge facing the tower. Cameras captured images every five minutes and an example of an individual image from the south-facing camera located on the northern edge of the study pasture is shown in Figure 2. Bison locations at the half-hourly time interval of the eddy covariance measurements were estimated by manually attributing bison locations to squares in a 20 m grid overlaid on the pasture area (Figure 1). The 20 m grid size represents the grid that we felt that we were able to attribute bison locations given features of the field that could be identified by camera, and we treat these observations as an initial guess that is subject to uncertainty. We test the sensitivity of per-animal methane efflux estimates to bison location estimates as described in the *Spatial Uncertainty* section below.

Incident and outgoing shortwave and longwave radiation and thereby the net radiation were measured using a NR01 net radiometer (Hukseflux, Delft, The Netherlands) mounted 1.5 meters above ground level. A SR50 sonic distance sensor

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(Campbell Scientific Inc., Logan, UT, USA) was installed at 1.3 m to gauge snow depth, and air temperature and relative humidity were measured at 2.25 meters using a HMP45C probe (Vaisala, Vantaa, Finland). Average 0–30 cm soil moisture and temperature were collected using CS650 probes (Campbell Scientific). Meteorological variables were measured once per minute, and half-hourly averages were stored using a CR3000 datalogger (Campbell Scientific).

Three-dimensional wind velocity was measured using a CSAT-3 sonic anemometer (Campbell Scientific) at 2.0 m above the ground surface. Carbon dioxide mixing ratios were measured at 10 Hz using a LI-7200 closed-path infrared gas analyzer (LI-COR Biosciences, Inc.) with inlet placed at the same height as the center of the sonic anemometer. Methane mixing ratios were measured at 10 Hz using a LI-7700 open-path infrared gas analyzer (LI-COR Biosciences, Inc., Lincoln, NE, USA) with the center of the instrument likewise located at 2.0 m and a 22 cm horizontal offset from the sonic anemometer; open- and closed-path infrared gas analyzers for eddy covariance have similar performance in field settings (Detto et al., 2011; Deventer et al., 2019). We use the atmospheric convention in which flux from biosphere to atmosphere is positive. Measurements were made during winter daytime hours from 0700 to 1700 local time to avoid depleting the battery bank and to ensure sufficient light to estimate bison location using game cameras. Flux measurements began on November 14, 2017 and ended on February 14, 2018.

Bison are dangerous and will charge humans. Their presence complicated data retrieval and game camera upkeep; some high-frequency flux measurements were overwritten and cameras shut down during exceptionally cold periods, resulting in missing measurements. Simultaneous flux and photographic data were obtained for the January 7, 2018 to February 13, 2018 period excluding January 10, 2018 when instruments were obstructed by snowfall. Flux data without accompanying game camera footage were obtained for the periods from November 14 through 29, 2017 and December 31, 2017, through January 6, 2018.

2.3 Flux calculations

Methane and carbon dioxide fluxes were calculated using EddyPro (LI-COR Biosciences, Lincoln, NE, USA). Standard double rotation, block averaging, and covariance maximization with default processing options were applied. Spike removal was performed as described by Vickers and Mahrt (1997) and spikes were defined as more than 3.5 standard deviations from the mean mixing ratio for carbon dioxide and more than 8 standard deviations from the mean mixing ratio for methane given the expectation of intermittent methane spikes from the bison herd. The default drop-out, absolute limit, and discontinuity tests were applied using the default settings following recommendations by Dumortier et al. (2019), and the Moncrieff et al. (1997) and Moncrieff et al. (2004) low- and high-pass filters were applied. The Webb-Pearman-Leuning correction (Webb et al., 1980) was applied to calculate methane efflux using the open-path LI-7700 sensor. Estimates of storage flux in the 2 m airspace below the infrared gas analyzers were assumed to be minor and excluded from the flux calculation. Flux measurements for which the quality control flag was greater than 1 following Mauder and Foken (2004) (see also Foken et al., 2004) were discarded and the net effect of all corrections when bison were present was a methane flux reduction of 14%. Measurements that exceeded an absolute value of 1 μmol m^{-2} s^{-1} for the case of methane flux and 20 μmol m^{-2} s^{-1} for the case of carbon dioxide flux were discarded following an analysis of the probability distribution of observations. We tested the sensitivity of flux measurements to the friction velocity ($u*$) to see if measurements made under conditions of insufficient turbulence should be excluded from the analysis despite the daytime-only flux measurement approach.

2.4 Flux footprint modelling

The eddy covariance flux footprint was calculated using the approach of Hsieh et al. (2000) extended to two dimensions following Detto and Katul (2006). Such analytical footprint models have been found to give minimally biased estimates of point-source fluxes in field settings (Dumortier et al., 2019). We performed the footprint analysis on a 1 m grid and aggregated values to the 20 × 20 m grid to which the bison locations were estimated (Figure 1). To further characterize the uncertainty in our per-animal methane flux estimates, described next, we also applied the flux footprint parameterization method of Kljun et al. (2015) aggregated to the same 20 × 20 m grid. The Kljun et al. (2015) model performs well in point-source experiments (Heidbach et al., 2017) and is widely used by the flux community. Figure 3 demonstrates an example of flux footprints for both models for a single half-hourly period.

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The momentum roughness height (z_{0m}) is required by both footprint models. Instead of assuming a constant z_{0m} over snow of 0.001 m (Andreas et al., 2004), we followed the approach of Baum et al. (2008) who calculated a unique z_{0m} for each half-hour eddy covariance measurement for a cattle feedlot system by rearranging the wind profile equation:

$$z_{0m} = \frac{z - d}{exp\left(ku/u_* + \psi_m\right)} \quad (1)$$

Where z is measurement height, u is wind speed, k is the von Karman constant, and ψ_m is the correction factor for atmospheric stability, here following Brutsaert (1982). The zero-plane displacement (d) for a field with obstacles is calculated following Verhoef et al. (1997):

$$d = z - \frac{z\left(1 - \exp\left(-\sqrt{42a}\right)\right)}{\sqrt{42a}}. \quad (2)$$

where a is the frontal area index of the obstacles (Raupach, 1994), here bison:

$$a = \frac{nbh}{S}. \quad (3)$$

The calculation of a uses the number of animals (n = 39), the size of the pasture (S, m^2), and the average breadth (b, m) and height (h, m) of the animals. We used established relationships for beef cattle as a function of weight (ASABE, 2006) given the lack of similar equations for bison. h was adjusted upward by 50% such that the height of adult males better-matched average values of fully-grown bison on the order of 1.8 m. The methane source location was assumed to be near the ground or snow surface per the typical posture of bison assuming that most methane efflux in ruminants is from erucation. We used the mean value of per-animal flux estimated by the two models and the variance between them to calculate footprint uncertainty.

2.5 Per-bison methane flux estimation

Given that mean methane emissions were not significantly different from zero in the absence of bison – as detailed in *Results* – we assume that observed methane emissions are due to bison in the flux footprint. The relative contribution of bison to each half-hourly eddy covariance measurement was calculated by expanding the approach of Dumortier et al. (2019) (see also Prajapati and Santos (2019)) for multiple point sources. From the definition of the footprint function (e.g. Schmid, 1997), the measured density of a scalar X, F_X, for our study area of 8 × 12 grid cells (Figure 1) is:

$$F_X = \sum_{i=1}^{8}\sum_{j=1}^{12} F_{ij}\phi_{ij}\Delta x_{ij}\Delta y_{ij} \quad (4)$$

where ϕ_{ij} is the value of the footprint function in grid cell ij and x and y are the dimensions of the 20 m grid cells (i.e. 400 m²). Dumortier et al. (2019) considered a known point source from a single cell, f_X, such that:

$$f_X = \frac{F_X}{\phi_{ij,source}} \quad (5)$$

where $\phi_{ij,source}$ is the value of the footprint function at the source location. We have n = 39 sources (i.e. bison) that are free to wander to any grid cell ij. We also have no basis for identifying individual bison given the resolution of the cameras, noting that this is possible using higher-resolution cameras (Merkle and Fortin, 2013) or GPS instruments. We also have no basis for determining if the methane sources of individual bison are different using our approach, so we must assume that methane efflux from each bison is equal. Under these assumptions we can write:

$$\langle f_x \rangle = \frac{F_X}{\sum_{i=1}^{8}\sum_{j=1}^{12} n_{ij}\phi_{ij}} \quad (6)$$

Where n_{ij} is the number of bison in grid cell ij (i.e. per 400 m^{-2}) and $\langle f_x \rangle$ is the average flux per bison. We only adopt this approach for calculating average methane efflux per bison as measured carbon dioxide fluxes in the absence of bison were greater than zero. Methane efflux values less than −200 µmol $bison^{-1}$ s^{-1} and greater than 300 µmol $bison^{-1}$ s^{-1} were treated as outliers and excluded based on an analysis of the probability distribution of observations.

2.6 Uncertainty estimation

The location of bison in the pasture was approximated visually by identifying the position of bison in relation to static cues in the study area using five-minute photographs. Observations were then aggregated to half-hourly flux measurement periods. This approach results in spatial uncertainty in bison location, especially due to movements within half-hourly periods and misallocation to nearby grid cells (Figure 1). We acknowledge that stochastic uncertainty is likely using our approach and explored the sensitivity of per-bison methane flux estimates to bison location using stochastic simulations in order to arrive at a conservative uncertainty estimates.

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The camera measurements resulted in many pixels where bison were not observed (e.g. Figure S1), but there is a finite probability that this absence was in error. Pixels near populated pixels likely have a higher probability that bison were located within them because small movements within half-hour periods were common and because their locations may have been misallocated due to measurement uncertainty. We therefore sought an approach that simulates a spatial distribution of bison that is constrained by the camera measurements. To do so, we treated the camera measurements as an initial guess of their location that helped us define a likelihood surface. The likelihood surface was determined using two-dimensional Tikhonov Regularization (Tikhonov and Arsenin, 1977), a classic mathematical technique to solve ill-posed problems, here the challenge of estimating the likelihood of bison location with intermittent and uncertain observations as described in detail in the Supplemental Information. The probability of the 39 bison landing in a pixel is informed by this likelihood surface, and we used 100 simulations for both the Hsieh et al. (2000) footprint and the Kljun et al. (2015) footprint along four different values of the spatial smoothness of the probability surface defined by the Lagrange multiplier (equation S1). An example of a likelihood surface generated for a single half-hour observation of bison locations and different values of the Lagrange multiplier is shown in Figure S1. We explore the sensitivity of per-bison methane emissions to the Tikhonov Regularization approach in the Supplemental Information (Figures S2 and S3).

We took the variance of the mean per-bison methane emissions from the 100 stochastic simulations as representative of uncertainty due to bison location. Uncertainty due to the flux footprint was calculated using

the variance of the mean per-bison flux calculated using the Hsieh et al. (2000) and Kljun et al. (2015) footprint models. Results are also to the eddy covariance methane flux measurements themselves, which range from 6 – 41% for half-hourly fluxes and 7 – 17% for long-term sums (Deventer et al., 2019). We use 17% as a representative uncertainty of eddy covariance sums as we are primarily concerned with providing a conservative assessment of uncertainty. Total uncertainty was calculated by summing variances calculated for the spatial uncertainty, footprint model uncertainty, and eddy covariance uncertainty. We suggest strategies for reducing uncertainty in the *Discussion* section.

3. Results

3.1 Meteorology

Air temperature averaged −2.8 °C and soil temperature averaged −0.3 °C during the measurement period (Figure 4A). Incident shortwave radiation ranged between 100 and 400 W m^{-2} during peak daylight hours (1000-1400 hours local time) across the study period, and clear conditions were common except for four weeks beginning in mid-December (Figure 4B). Snow depth within the tower enclosure increased from 0.15 m to nearly 0.4 m in late 2017 and decreased to 0.1 m beginning in late January 2018 (Figure 4C) noting that snow outside of the electrified tower enclosure was often trampled (see Figure 2). The mean (median) wind direction was 221° (208°) during periods when visible imagery of bison locations was available and eddy covariance measurements passed quality control checks (Figure 5).

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We applied the Tikhonov Regularization approach to each bison distribution map

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3.2 Gas flux

Half-hourly methane fluxes averaged 0.048 ± 0.081 µmol m^{-2} s^{-1} (mean ± standard deviation) and carbon dioxide fluxes averaged 1.6 ± 1.4 µmol m^{-2} s^{-1} when bison were present (Figure 6), noting again that measurements were made only during daytime periods. Methane flux in the absence of bison averaged −0.0009 ± 0.008 µmol m^{-2} s^{-1} and carbon dioxide flux averaged 0.64 ± 1.0 µmol m^{-2} s^{-1}, significantly lower than when bison were present ($P < 0.001$ for both CH_4 and CO_2). CO_2 flux was significantly related to methane flux and explained 52% of its variance when bison were present but only 7% when they were absent (Figure 7). CO_2 flux was significantly and positively related to air and soil temperature across the entire measurement record ($P < 0.001$ in both cases), but methane flux was not. There were no significant temporal patterns of methane flux during the daytime periods investigated here, and neither incident nor net radiation were related to methane flux. When bison were present, methane flux was not significantly different during days when feed was delivered (0.051 ± 0.083 µmol m^{-2} s^{-1}) and days when it was not (0.035 ± 0.10 µmol m^{-2} s^{-1}) ($P = 0.075$).

Methane flux was significantly and positively related to friction velocity in the absence of bison at $u*$ values greater than 0.2 m s^{-1} ($P = 0.003$) but not positively related to $u*$ values less than 0.2 m s^{-1}, indicating that flux measurements were unrelated to friction velocity values commonly associated with insufficient turbulence (Figure 8A). Carbon dioxide flux was not related to $u*$ in the absence of bison (Figure 8B) but negative values were observed at $u*$ values greater than 0.45 m s^{-1}. Given these observations, we did not apply a $u*$ filter to our eddy covariance measurements, which were made only during daytime periods. We discuss potential reasons for the observed increase in methane flux and negative CO_2 flux with high values of $u*$ in the *Discussion* section.

3.3 Bison location and methane efflux

Timelapse camera footage yielded usable imagery for 444 half-hourly periods of which 245 half-hourly periods had available eddy covariance observations and of which 177 had eddy covariance measurements that passed quality control criteria. Bison tended to aggregate in an area on the west side of the pasture near the location where supplemental hay was often provided (Figure 9A). They intermittently visited the area north of the tower in mornings and afternoons and intermittently made sporadic mass movements to the southernmost edge of the field near its gate during midday periods (Figure 9B-D).

Bison were located within the 90% flux footprint 40% of the time (Figure 10). There was an average of eight (seven) bison within the 90% flux footprint of the Hiseh et al. (2000) (Kljun et al. (2015)) models. When excluding periods for which bison were absent from the flux footprint, this value increased to 21 (20), respectively (Figure 10). Per-bison methane emission estimates when using the Hsieh et al. (2000) footprint model had a mean (± standard error) of 55 ± 0.96 µmol bison^{-1} s^{-1} and a median of 29 µmol bison^{-1} s^{-1} as a result of the positively skewed measurement distribution (Figure 11A). These estimates are 11% lower than per-bison methane emission estimates from the Kljun et al. (2015) footprint model, which returned a mean (± standard error) of 62 ± 0.91 µmol bison^{-1} s^{-1}, which demonstrates that per-animal flux estimates are sensitive to flux footprint methodology.

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Per-bison methane flux estimates from stochastic simulations of bison location were sensitive to the smoothness of the likelihood surface (Figure 12). Combining per-bison methane flux estimates from all 100 simulations resulted in a standard deviation of 6.2 μmol bison^{-1} s^{-1} when using the Hsieh et al. (2000) model and 5.8 μmol bison^{-1} s^{-1} when using the Kljun et al. (2015) model. If we sum variances to combine uncertainties due to spatial uncertainty, flux footprint, and the eddy covariance measurements themselves, we arrive at a combined standard deviation of 8.3 μmol bison^{-1} s^{-1}, which is dominated uncertainty due to bison location (50% of the total uncertainty), then the flux footprint model (36%), then the eddy covariance measurements (14%).

4 Discussion

The eddy covariance flux footprint analysis coupled to bison location estimates from automated camera images resulted in a mean (median) methane flux of 55 (29) μmol bison^{-1} s^{-1} when applying the Hsieh et al. (2000) footprint model and 62 (43) μmol bison^{-1} s^{-1} when applying the Kljun et al. (2015) footprint model for a combined mean (median) ± standard deviation of 58.5 (36) ± 8.3 μmol bison^{-1} s^{-1}, or 81 ± 11.5 g CH_4 bison^{-1} day^{-1}. Measurements were made during daytime periods in winter and are sensitive to estimates of bison location (Figure 12). If we naively assume that methane flux from bison varies negligibly across the full diurnal and seasonal range, a notion that needs to be substantiated, our measurements with conservative uncertainty estimates correspond to 29.6 ± 4.2 kilograms of methane per bison per year, noting that methane emissions from cattle have been observed to be on the order of 10-17% higher in summer than winter (Todd et al., 2014; Prajapati and Santos, 2018; Prajapati and Santos, 2019) but lower in evenings if animals eat less during these times (Gao et al., 2011).

The mean bison mass of the study herd was 329 kg, similar to the 300 kg buffalo that is assumed to emit 55 kg year^{-1} in the 2006 IPCC report (IPCC 2006) noting that dairying buffalo cows are estimated to have higher methane emissions than other buffalo (Cóndor et al. 2008). The study herd comprised numerous pregnant females (Table S1) that have higher metabolic requirements. Previous estimates of methane emissions from range cattle are on the order of 60 kg per year per animal (Hogan, 1993), about twice as large as the mean per-bison methane flux calculated here. Values were instead similar to lower-range measurements from young heifers feeding on ryegrass of 88 g CH_4 animal^{-1} day^{-1} (Hammond et al., 2016) and wintertime measurements of beef cattle in a feedlot on the order of 75 g CH_4 animal^{-1} day^{-1} (Prajapati and Santos, 2019). In other words, while there is no evidence from our measurements that bison have more or less methane efflux than typical values reported for cattle, it is critical to make full year-round methane flux measurements with uncertainty to understand the seasonal course of bison methane efflux to establish defensible annual sums. Below, we discuss potential reasons for the relatively low bison methane emissions observed here as well as a strategy for reducing uncertainty in eddy covariance measurements of methane efflux from grazing non-domesticated ruminants.

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4.1 Methane and carbon dioxide efflux in response to environmental variables and bison presence

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Methane flux was not related to air or soil temperature but was related to u^* – especially at relatively high values of u^* – in the absence of bison (Figure 8). These observations are consistent with a potential pressure pumping mechanism for trace gases through snow at higher wind speeds (Bowling and Massman, 2011) although it is unclear why this relationship exists for methane flux and not carbon dioxide flux as is frequently found in snow-covered conditions (Rains et al., 2016). Carbon dioxide flux at high values of u^* was negative indicating net CO_2 uptake by the biosphere, which is unlikely in our study site during winter, suggesting that values with excessively high u^* may need to be filtered, but with only five observations of CO_2 flux less than zero it is unclear how to apply such a filter in our case.

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Insufficient evidence exists in our data record to attribute observed methane efflux to the onset of freezing conditions in soil (Mastepanov et al., 2008). We note that extensive snow trampling (e.g., Figure 2) likely resulted in a situation where snow depth (Figure 4C) and its insulating effect on soil temperature (Figure 4A) varied across the field and therefore differed from snow and soil measurements taken within the instrumentation enclosure. Regardless, mean methane flux when bison were absent, −0.0009 µmol m^{-2} s^{-1}, was nearly two orders of magnitude less than the mean methane flux when bison were present, 0.041 µmol m^{-2} s^{-1}. Whereas we cannot exclude – and in fact expect – non-zero background methane fluxes from non-bison sources in a grassland in winter in the vicinity of a riparian area (Figure 1, Merbold et al., 2013; McLain and Martens, 2006; Mosier et al., 1991), these are minor compared to the CH_4 flux attributable to bison (Figures 6 and 7). Bison are associated with a distinct methane flux signature as shown by the immediate decline of methane fluxes following their removal from the study pasture (Figure 6) and strong relationship with carbon dioxide flux (Figure 7) given the common source of respiration and most enteric methane losses from the muzzles of ungulates. Methane flux was related to carbon dioxide flux when bison were present or absent (Figure 7), suggesting both soil and ruminant sources (and in the case of methane sinks) of both gases (Baldocchi et al., 2012; Gourlez de la Motte et al., 2019).

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It is important to note that potential methane fluxes from bison manure may have been dampened by freezing conditions but may be an important methane source during warmer conditions if it enters anoxic conditions. Manure is thought to contribute a nontrivial portion (10-14 Tg CH_4 yr^{-1}) of total global ruminant methane efflux (77 Tg CH_4 yr^{-1}, Johnson and Ward 1996; Moss et al., 2000) noting that some farm-scales studies arrive at lower percentages (Taylor et al., 2017). Though we did not observe higher methane efflux early in the study period when soil temperature was above freezing nor temperature sensitivity of methane efflux in the presence or absence of bison, it is important to note that field-scale methane efflux may be diminished by the thermal environment of manure in our measurements but is still likely to be relatively low in a rangeland setting (Steed Jr. and Hashimoto, 1994).

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4.2 Bison spatial distribution and measurement uncertainty

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Ruminant behavior is critical to track to estimate field-scale efflux (Gourlez de la Motte et al., 2019). The spatial distribution of bison in the study pasture varied from morning to midday and afternoon (Figure 9). It is difficult to infer from the available

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data whether the study bison are more active during morning and evening hours in the pasture environment like cattle (Gregorini 2012). Supplemental hay was made available to the bison approximately 50 meters west of the tower and increases in the frequency of bison appearance there are associated with the animals' preferred feeding times after dawn and before dusk, but observed methane flux did not vary as a function of time of day (e.g. Dengel et al. 2011) and was not significantly different during days when hay was provided and when it was not, noting that the animals were free to also graze on vegetation within the pasture. Regardless, ruminant methane flux measurements are simpler to make when animals congregate (Coates et al., 2017; Tallec et al., 2012) as was often observed here (e.g. Figures 2, 9 & 10). Aggregation behavior in our study bison herd was often upwind of the eddy covariance tower (Figures 5 & 9) and resulted in more overlap between flux footprint and bison location than would have occurred if bison locations were randomly distributed throughout the study area, emphasizing the importance of tower placement in eddy covariance studies of grazing systems.

Despite the largely favorable location of the herd with reference to wind direction and the flux footprint, spatial uncertainties in bison location dominated the total uncertainty calculated here More accurate location observations are a logical way to reduce this uncertainty. Uncertainties in flux footprint modelling for methane source attribution were also non-trivial on the order of 36%. Footprint models of the type used here have been found to accurately estimate point sources of trace gas flux (Heidbach et al., 2017; Dumortier et al., 2019), but it is important to note that footprint modelling techniques play a large role in the spatial attribution of observed fluxes of ruminant trace gas flux (Felber et al., 2015). Prajapati and Santos (2018), for instance, found that an analytical model (Kormann and Meixner 2001) predicted flux footprint areas five to six times larger than did an approximation of a Lagrangian dispersion model (Kljun et al., 2002), such that footprint model uncertainty is a major source of uncertainty for measuring methane flux from multiple point sources as we also found here. Regarding the footprint model it is also important to note that emitted gas is warmer than the surrounding environment in our case. It is unclear how well typical eddy covariance flux footprint models simulate the release location of heated parcels noting but we note that heat is also transferred more efficiently than passive scalars like methane in the convective sublayer (Katul et al., 1995) such that methane transport should not be assumed to behave like heat. It is also unclear for our case if a point near the snow surface accurately represented the typical parcel release height. We were unable to track individual animals with different muzzle heights, noting that the animals were also frequently grazing with muzzle below the snow surface such that the true parcel release point represented a wide range of heights that we had little basis to simulate from available observations.

4.3 Future directions for greenhouse gas accounting in ruminant grazing systems

Methane efflux cannot be completely removed from ruminant grazing systems; some 4.6 – 6.2% of gross energy intake is lost as methane in cattle, sheep and goats worldwide (Johnson and Ward 1996) with cattle often falling on the higher end of the observed range (Lassey et al., 1997). But there are other aspects of bison ecology that merit consideration when designing greenhouse gas-cognizant grazing systems. For example, cattle tend to graze close to water more frequently than bison do (Allred et al., 2011) with unclear consequences for riparian vegetation, water quality, and potential methane efflux from

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wallows. Cattle also tend to graze for longer periods than bison (Plumb and Dodd, 1993) and it is unclear if there is an associated consequence for methane efflux. Future work should consider the large inter-animal variability in methane efflux (Lassey et al., 1997), possibly using advanced techniques for identifying individual animals through photographs (Merkle and Fortin, 2013) or tracking devices (Felber et al., 2015). Animal age and size are also important factors in ruminant methane efflux (Jiao et al., 2014) and individual tracking may improve our estimates of this variability in a field setting. That being said it will be difficult to measure the methane contributions of individual animals in species that tend to herd using eddy covariance Adding seasonal foraging behavior, estimating emissions from individual animals, and addressing seasonal and inter-annual variability and trends in forage nutrition are likely to further improve prediction of methane emissions from grazing systems (Moraes et al., 2013). Advanced eddy covariance algorithms are also likely to improve flux estimates on short time scales noting that non-stationary bursts have not been found to create systematic bias in methane budgets measured over longer time periods using eddy covariance (Göckede et al., 2019). Of these, advanced footprint attribution techniques like Environmental Response Functions designed to create improved maps of surface-atmosphere fluxes (Metzger et al., 2013; Xu et al., 2017) may be uniquely applicable to the challenging case presented by grazing systems with mobile point sources and intermittent biogeochemical hotspots created by animal waste. Going forward, increases in atmospheric carbon dioxide concentrations are likely to decrease forage quality (Jégo et al., 2013), resulting in higher leaf carbon to nitrogen ratios and increasing ruminant methane emissions (Lee et al., 2017), all else being equal. Understanding greenhouse gas fluxes from ruminants is therefore likely to be even more important in the future. An ongoing interest in bison reintroduction and ungulate ecology coupled with established micrometeorological measurement techniques will help us understand the present and future role that bison and other alternative grazing systems play in the Earth system.

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Code/Data availability

Eddy covariance and micrometeorological data have been submitted to Ameriflux for publication at https://ameriflux.lbl.gov/sites/siteinfo/US-Tur.

Author contributions

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The land managers provided information that describes bison age, sex, weight, and pregnancy status (Table S1) and the composition (Table S2) and the delivery schedule (Table S3) of hay. ¶

PCS designed the study with AC, JD, and WK and wrote the manuscript with all coauthors. AC collected data and analyzed it with PCS and TG. NK assisted with the footprint analysis.

Competing interests

The authors declare no competing interests.

References

Allred, B. W., Fuhlendorf, S. D. and Hamilton, R. G.: The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere 2(3), 26, 2011.

Andreas, E. L., Jordan, R. E., Guest, P. S., Persson, O. G., Grachev, A. A., and Fairall, C. W.: Roughness lengths over snow. In 18th Conference on Hydrology of the American Meteorological Society, Seattle, WA, 11–15 January, 2004.

Baldocchi, D. D., Detto, M., Sonnentag, O., Verfaillie, J., Teh, Y. A., Silver, W. and Kelley, N. M.: The challenges of measuring methane fluxes and concentrations over a peatland pasture. Agric. For. Met. 153, 177-187, 2012.

Baum, K. A., Ham, J. M., Brunsell, N. A. and Coyne, P. I.: Surface boundary layer of cattle feedlots: Implications for air emissions measurement. Ag. Forest. Met. 148, 1882-1893, 2008.

Beauchemin, K. A., Kreuzer, M., O'Mara, F. and McAllister, T. A.: Nutritional management for enteric methane abatement: a review, Aust. J. Exp. Agric., 48(2), 21–27, 2008.

Boadi, D. A. and Wittenberg, K. M.: Methane production from dairy and beef heifers fed forages differing in nutrient density using the sulphur hexafluoride (SF_6) tracer gas technique. Can. J. Anim. Sci., 82, 201-206, 2002.

Bowling, D. R. and Massman, W. J.: Persistent wind-induced enhancement of diffusive CO_2 transport in a mountain forest snowpack. J. Geophys. Res. 116, 1–15, 2011.

Brutsaert, W.: Evaporation into the Atmosphere: Theory, History, and Applications. Dordrecht: Kluwer, 1982.

Chappellaz, J. A., Fung, I. Y. and Thompson A. M.: The atmospheric CH_4 increase since the Last Glacial Maximum. Tellus B, 45(3), 228-241, 1993.

Chaves, A. V., Thompson, L., C., Iwaasa, A., D., Scott, S., L., Olson, M. E., Benchaar, C., Veira, D., M. and McAllister, T., A.: Effect of pasture type (alfalfa vs. grass) on methane and carbon dioxide production by yearling beef heifers. Can. J. Anim. Sci., 86, 409-418, 2006.

Coates, T., W., Benvenutti, M. A., Flisch, T. K., Charmley, E., McGinn, S. M. and Chen D.: Applicability of eddy covariance to estimate methane emissions from grazing cattle. J. Environ. Qual. 47(1), 54-61, 2017.

Collins, S.L. and Steinauer, E.M.: Disturbance, diversity and species interactions in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SC (ed) Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, pp 140–156, 1998.

Cóndor, R. D., Valli, L., De Rosa, G., Di Francia, A. and De Lauretis, R: Estimation of the methane emission factor for the Italian Mediterranean buffalo. Animal 2:8, 1247–1253, 2008.

Coppedge, B. R. and Shaw, J. H.: Bison grazing patterns on seasonally burned tallgrass prairie. J. Range Manage. 51, 258-264, 1998.

Crutzen, P. J., Aselmann, I. and Seiler, W.: Methane production by domestic animals, wild ruminants, other herbivorous fauna, and humans. Tellus B 38, 271-284, 1985.

Dengel, S., Levy, P. E., Grace, J., Jones, S. K. and Skiba, U. M.: Methane emissions from sheep pasture, measured with an open-path eddy covariance system, Glob. Chang. Biol. 17(12), 3524–3533, 2011.

DeRamus, H.A., Clement, T.C., Giampola, D.D. and Dickison, P.C.: Methane emissions of beef cattle on forages. J. Environ. Qual.: 32(1), 269-277, 2003.

Detto, M. and Katul, G. G.: Simplified expressions for adjusting higher-order turbulent statistics obtained from open path gas analyzers, Bound.-Layer Meteorol., 122(1), 205–216, 2006.

Detto, M., Verfaillie, J., Anderson, F., Xu, L. and Baldocchi, D.: Comparing laser-based open- and closed-path gas analyzers to measure methane fluxes using the eddy covariance method, Agric. For. Meteorol., 151(10), 1312–1324, 2011.

FAO: Global Livestock Environmental Assessment Model (GLEAM). Rome, 2017.

Deventer, M. J., Deventer, M., Griffis, T. J., Roman, D., Kolka, R. K., Wood, J. D., Erickson, M., Baker, J. M. and Millet, D. B.: Error characterization of methane fluxes and budgets derived from a long-term comparison of open- and closed-path eddy covariance systems, Agricultural and Forest Meteorology, 278, 107638, 2019.

Dumortier, P., Aubinet, M., Lebeau, F., Naiken, A. and Heinesch, B.: Point source emission estimation using eddy covariance: Validation using an artificial source experiment. Agric. For. Meteorol., 266-267, 148-156, 2019.

Felber, R., Münger, A., Neftel, A. and Ammann, C.: Eddy covariance methane flux measurements over a grazed pasture: effect of cows as moving point sources, Biogeosciences, 12(12), 3925–3940, 2015.

Flores D: Bison ecology and bison diplomacy: The southern plains from 1800 to 1850. J Am Hist 78:465–485, 1991.

Fortin, D., Fryxell, J. M., O'Brodovich, L. and Frandsen, D.: Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles, Oecologia, 134(2), 219–227, 2003.

Freese, C. H., Aune, K. E., Boyd, D. P., Derr, J. N., Forrest, S. C., Gates, C. C., Gogan, P. J. P., Grassel, S. M., Halbert, N., D., Kunkel, K. and Redford, K., H.: Second chance for the plains bison. Biological Conservation, 136(2), 175-184, 2007.

Galbraith, J. K., Mathison, G. W., Hudson, R. J., McAllister, T. A. and Cheng, K.-J.: Intake, digestibility, methane and heat production in bison, wapiti and white-tailed deer, Can. J. Anim. Sci., 78(4), 681–691, 1998.

Foken T., Göckede, M., Mauder, M., Mahrt, L., Amiro, B. and Munger W.: Post-field data quality control. In Lee, X., Massman, W.J. and Law, B. (eds) Handbook of micrometeorology: A guide for surface flux measurement and analysis. Kluwer, Dordrecht, The Netherlands, 2004.

Gates, C. C., Freese, C. H., Gogan, P. J. and Kotzman M (eds): American bison: status survey and conservation guidelies 2010. IUCN, 2010.

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Gerber, P.J., Steinfeld, H., Henderson, B., Mottet, A., Opio, C., Dijkman, J., Falcucci, A. and Tempio, G.: Tackling climate change through livestock - A global assessment of emissions and mitigation opportunities. Food and Agriculture Organization of the United Nations (FAO), Rome, 2013.

Geremia, C, Merkle, J.A., Eaker, D.R., Wallen, R.L., White, P.J., Hebblewhite, M. and Kaufman, M.J.: Migrating bison engineer the green wave. Proc. Nat. Acad. Sci.: 116(51), 25707-25713, 2019.

Gregorini, P. Diurnal grazing pattern: its physiological basis and strategic management. Animal Production Science 52.7: 416-430, 2012.

Göckede, M., Kittler, F. and Schaller, C.: Quantifying the impact of emission outbursts and non-stationary flow on eddy-covariance CH_4 flux measurements using wavelet techniques, Biogeosciences, 16, 3113–3131, 2019.

Gourlez de la Motte, L., Dumortier, P., Beckers, Y., Bodson, B., Heinesch, B. and Aubinet, M.: Herd position habits can bias net CO_2 ecosystem exchange estimates in free range grazed pastures, Agric. For. Met. 268, 156–168, 2019.

Hammond, K.J., Jones, A.K., Humphries, D.J., Crompton, L.A. and Reynolds, C.K.: Effects of diet forage source and neutral detergent fiber content on milk production of dairy cattle and methane emissions determined using GreenFeed and respiration chamber techniques. J. Dairy Sci. 99: 7904-7917, 2016.

Hanson, J.R.: Bison ecology in the Northern Plains and a reconstruction of bison patterns for the North Dakota region. Plains Anthropol., 93–113, 1984.

Hartnett, D.C., Hickman, K.R. and Fischer, W.L.E.: Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. J. Range. Manage., 49, 413-420, 1996.

Hedrick, P. W.: Conservation genetics and North American bison (*Bison bison*), J. Hered., 100(4), 411–420, 2009.

Hogan, K. B.: Anthropogenic methane emissions in the United States: Estimates for 1990. National Service Center for Environmental Publications, 1993.

Herrero, M., Henderson, B., Havlík, P., Thornton, P. K., Conant, R. T., Smith, P., Wirsenius, S., Hristov, A. N., Gerber, P., Gill, M., Butterbach-Bahl, K., Valin, H., Garnett, T. and Stehfest, E.: Greenhouse gas mitigation potentials in the livestock sector, Nature Climate Change, 6(5), 452–461, doi:10.1038/nclimate2925, 2016.

Heidbach, K., Schmid, H.-P., and Mauder, M.: Experimental evaluation of flux footprint models. Agric. For. Meteorol. 246: 142-153.

Hristov, A.N.: Historic, pre-European settlement, and present-day contribution of wild ruminants to enteric methane emissions in the United States. J. Animal Sci.: 90(4), 1371-1375, 2012.

Hristov, A. N., Oh, J., Firkins, J. L., Dijkstra, J., Kebreab, E., Waghorn, G., Makkar, H. P. S., Adesogan, A. T., Yang, W., Lee, C., Gerber, P. J., Henderson, B. and Tricarico, J. M.: Special topics — Mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options, Journal of Animal Science, 91(11), 5045–5069, doi:10.2527/jas.2013-6583, 2013.

Hsieh, C.-I., Katul, G. and Chi, T.-W.: An approximate analytical model for footprint estimation of scalar fluxes in thermally stratified atmospheric flows, Adv. Water Resour., 23(7), 765–772, 2000.

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Intergovernmental Panel on Climate Change: Emissions from livestock and manure management. *2006 IPCC guidelines for national greenhouse gas inventories*, 2006.
Isenberg, A.C. The Destruction of the Bison: An Environmental History, 1750–1920. Cambridge Univ Press, Cambridge, UK, 2000.
Jégo, G., Bélanger, G., Tremblay, G. F., Jing, Q. and Baron, V. S.: Calibration and performance evaluation of the STICS crop model for simulating timothy growth and nutritive value, Field Crops Res., 151, 65–77, 2013.
Jiao, H., Yan, T., Wills, D. A., Carson, A. F. and McDowell, D. A.: Development of prediction models for quantification of total methane emission from enteric fermentation of young Holstein cattle at various ages. *Agriculture, Ecosystems & Environment*, 183, 160-166, 2014.
Johnson, K. A. and Johnson, D. E.: Methane emissions from cattle. J. Anim. Sci., 73, 2483-2491, 1995.
Johnson, D. E. and Ward, G. M.: Estimates of animal methane emissions. Environ. Monit. Assess., 42, 133-141, 1996.
Katul, G., Goltz, S.M., Hsieh, C.I., Cheng, Y., Mowry, F. and Sigmon, J.: Estimation of surface heat and momentum fluxes using the flux-variance method above uniform and non-uniform terrain. *Boundary-Layer Meteorology*, 74(3), 237-260, 1995.
Kelliher, F. M. and Clark, H.: Methane emissions from bison—An historic herd estimate for the North American Great Plains, Agric. For. Meteorol., 150(3), 473–477, 2010.
Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J. G., Dlugokencky, E. J., Bergamaschi, P., Bergmann, D., Blake, D. R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E. L., Houweling, S., Josse, B., Fraser, P. J., Krummel, P. B., Lamarque, J.-F., Langenfelds, R. L., Le Quéré, C., Naik, V., O'Doherty, S., Palmer, P. I., Pison, I., Plummer, D., Poulter, B., Prinn, R. G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D. T., Simpson, I. J., Spahni, R., Steele, L. P., Strode, S. A., Sudo, K., Szopa, S., van der Werf, G. R., Voulgarakis, A., van Weele, M., Weiss, R. F., Williams, J. E. and Zeng, G.: Three decades of global methane sources and sinks, Nat. Geosci., 6(10), 813–823, 2013.
Kljun, N., Rotach, M.W., Schmid, H.P.: A 3D Backward Lagrangian Footprint Model for a Wide Range of Boundary Layer Stratifications. Boundary-Layer Meteorology 103, 205-226, 2002.
Kljun, N., Calanca, P., Rotach, M.W., Schmid, H.P.: A simple two-dimensional parameterisation for Flux Footprint Prediction (FFP), Geoscientific Model Development, 8, 3695-3713, 2015.
Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C. and Towne, G. E.: The keystone role of bison in North American tallgrass prairie, Bioscience, 49(1), 39, 1999.
Kormann, R. and Meixner F. X.. An analytical footprint model for non-neutral stratification. Bound.-Layer Meteorol., 99(2), 207-224, 2001.
Lassey, K. R., Ulyatt, M. J., Martin, R. J., Walker, C. F. and Shelton, I., D.: Methane emissions measured directly from grazing livestock in New Zealand. Atmos. Environ. 31, 2905-2914, 1997.
Lee, M. A., Davis, A. P., Chagunda, M. G. G. and Manning, P.: Forage quality declines with rising temperatures, with implications for livestock production and methane emissions, Biogeosciences, 14, 1403-1417, 2017.

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Mastepanov, M., Sigsgaard, C., Dlugokencky, E. J., Houweling, S., Ström, L., Tamstorf, M. P. and Christensen, T. R.: Large tundra methane burst during onset of freezing. Nature, 456, 628–631, 2008.

Mauder, M., and Foken, T.: Documentation and instruction manual of the eddy-covariance software package TK3, 2011.

McLain, J.E. and Martens, D.A.: Moisture controls on trace gas fluxes in semiarid riparian soils. Soil Sci. Soc. Am. J. 70(2), 367-77, 2006.

Merbold, L., Steinlin, C. and Hagedorn, F.: Winter greenhouse gas fluxes (CO_2, CH_4 and N_2O) from a subalpine grassland. Biogeosciences. 10(5), 3185-3203, 2013.

Metzger, S., Junkermann, W., Mauder, M., Butterbach-Bahl, K., Trancón y Widemann, B., Neidl, F., Schäfer, K., Wieneke, S., Zheng, X.H., Schmid, H.P. and Foken, T.: Spatially explicit regionalization of airborne flux measurements using environmental response functions. Biogeosciences, 10(4), 2193-2217, 2013.

Merkle, J. A. and Fortin D.: Likelihood-based photograph identification: Application with photographs of free-ranging bison. Wild. Soc. Bull., 38, 196-204, 2014.

Moncrieff, J., Clement, R., Finnigan, J., and Meyers, T.: Averaging, detrending, and filtering of eddy covariance time series. In Lee, X., Massman, W.J. and Law, B. (eds) Handbook of Micrometeorology. Springer, Dordrecht, 7-31, 2004.

Moncrieff, J.B., Massheder, J.M., De Bruin, H., Elbers, J., Friborg, T., Heusinkveld, B., Kabat, P., Scott, S., Søgaard, H., and Verhoef, A.: A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. J. Hydrology, 188, 589-611, 1997.

Moraes, L. E., Strathe, A. B., Fadel, J. G., Casper, D. P. and Kebreab, E.: Prediction of enteric methane emissions from cattle. Glob. Change Biol., 20, 2140-2148, 2014.

Moe, P. W. and Tyrrell, H. F.: Methane production in dairy cows, J. Dairy Sci., 62(10), 1583–1586, 1979.

Mosier, A., Schimel, D., Valentine, D., Bronson, K. and Parton, W. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. Nature, 350(6316), 330-332, 1991.

Moss, A.R., Jouany, J.-P., and Newbold, J.: Methane production by ruminants: its contribution to global warming. Ann. Zootech., 49, 231-253, 2000.

Nisbet, E. G., Manning, M. R., Dlugokencky, E. J., Fisher, R. E., Lowry, D., Michel, S. E., Lund Myhre, C., Platt, S. M., Allen, G., Bousquet, P., Brownlow, R., Cain, M., France, J. L., Hermansen, O., Hossaini, R., Jones, A. E., Levin, I., Manning, A. C., Myhre, G., Pyle, J. A., Vaughn, B. H., Warwick, N. J. and White, J. W. C.: Very strong atmospheric methane growth in the 4 Years 2014–2017: Implications for the Paris Agreement, Glob. Biogeochem. Cycles, 33(3), 318–342, 2019.

Pereira D.: Wind Rose (https://www.mathworks.com/matlabcentral/fileexchange/47248-wind-rose), MATLAB Central File Exchange. Retrieved May 27, 2020.

Plumb, G. E. and Dodd J. L.: Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecol. App. 3, 631– 643, 1993.

Prajapati, P. and Santos, E. A.: Estimating methane emissions from beef cattle in a feedlot using the eddy covariance technique and footprint analysis, Agric. For. Meteorol., 258, 18–28, 2018.

Rains, F. A., Stoy, P. C., Welch, C. M., Montagne, C. & McGlynn, B. L.: A comparison of methods reveals that enhanced diffusion helps explain cold-season soil CO_2 efflux in a lodgepole pine ecosystem. Cold Regions Science and Technology, 121, 16-24, 2016.

Reisinger, A. and Clark, H.: How much do direct livestock emissions actually contribute to global warming? Glob. Chang Biol. 24(4), 1749-1761, 2018.

Sanderson, E.W., Redford, K.H., Weber, B., Aune, K., Baldes, D., Berger, J., Carter, D., Curtin, C., Derr, J., Bodrott, S., Fearn, E., Fleener, C., Forrest, S., Gerlach, C., Gates, C. C. Gross, J. E., Gogan, P., Grassel, S., Hilty, J.A., Jensen, M., Kunkel, K., Lammers, D., List, R., Minowski, K., Olson, T., Pague, C., Robertson, P. and Stephenson, B.: The ecological future of the North American Bison: Conceiving long-term, large-scale conservation of wildlife, Conservation Biology 22(2), 252-266, 2008.

Schmid, H.P.: Experimental design for flux measurements: matching scales of observations and fluxes. Agric. For. Meteorol., 87, 179–200, 1997.

Smith, F. A., Hammond, J. I., Balk, M. A., Elliott, S., M., Lyons, S., K., Pardi, M., I., Tomé, C. P., Wagner, P., J. and Westover, M., L.: Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. Proc. Natl. Acad. Sci. U. S. A., 113 (4), 874-879, 2016.

Smits, D. D.: The frontier army and the destruction of the buffalo: 1865-1883. West. Hist. Q., 25, 313–338, 1994.

Steed Jr, J. and Hashimoto, A. G.: Methane emissions from typical manure management systems. Bioresource Technology, 50(2), 123-130, 1994.

Steuter, A. A. and Hidinger, L.: Comparative ecology of bison and cattle on mixed-grass prairie. Great Plains Research 9:329–342, 1999.

Stoy, P. C. and Quaife T.: Probabilistic downscaling of remote sensing data with applications for multi-scale biogeochemical flux modeling. PLoS One, 10(6): e0128935, 2005.

Subak, S.: Methane from the House of Tudor and the Ming Dynasty: Anthropogenic emissions in the sixteenth century. Chemosphere, 29(5), 843-854, 1994.

Sun, K., Tao, L., Miller, D. J., Zondlo, M. A., Shonkwiler, K. B., Nash, C. and Ham, J. M.: Open-path eddy covariance measurements of ammonia fluxes from a beef cattle feedlot, Agric. For. Meteorol., 213, 193–202, 2015.

Tallec, T., Klumpp, K., Hensen, A., Rochette, Y. and Soussana, J.-F.: Methane emission measurements in a cattle grazed pasture: a comparison of four methods. Biogeosciences Discussions, doi.org/10.5194/bgd-9-14407-2012, 2012.

Taylor, A. M., Amiro, B. D., Tenuta, M. and Gervais, M.: Direct whole-farm greenhouse gas flux measurements from a beef cattle operation. Agr. Ecosyst. Environ., 239, 65-79, 2017.

Thompson, A. M., Chappellaz, J. A., Fung, I. Y. and Kucsera, T. L.: The atmospheric CH_4 increase since the Last Glacial Maximum, Tellus B Chem. Phys. Meteorol., 45(3), 242–257, 1993.

Tikhonov, A.N. and Arsenin, V.Y.: Solutions of ill-posed problems. Washington, D.C.: Winston, 1977.

Thornton, P. K. and Herrero, M.: Potential for reduced methane and carbon dioxide emissions from livestock and pasture management in the tropics, Proc. Natl. Acad. Sci. U. S. A., 107(46), 19667–19672, 2010.

Todd, R. W., Altman, M. B., Cole, N. A. and Waldrip, H. M.: Methane emissions from a beef cattle feedyard during winter and summer on the Southern High Plains of Texas, J. Environ. Qual., 43, 1125-1130, 2014.

Towne, E.G., Hartnett, D.C., Cochran, R.C.: Vegetation trends in tallgrass prairie from bison and cattle grazing, Ecol. Appl., 15, 1550–1559, 2005.

Vickers, D. and Mahrt, L.: Quality control and flux sampling problems for tower and aircraft data, J. Atmos. Ocean. Technol., 14(3), 512–526, 1997.

Vinton, M. A., Hartnett, D. C., Finck, E. J. and Briggs, J. M.: Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie, Am. Midl. Nat., 129(1), 10, 1993.

Webb, E. K., Pearman, G. I. and Leuning, R.: Correction of flux measurements for density effects due to heat and water vapour transfer, Quarterly Journal of the Royal Meteorological Society, 106(447), 85–100, 1980.

Wolf, J., Asrar, G. R. and West, T. O.: Revised methane emissions factors and spatially distributed annual carbon fluxes for global livestock, Carbon Balance Manag., 12(1), 16, 2017.

Xu, K., Metzger, S. and Desai, A.R.: Upscaling tower-observed turbulent exchange at fine spatio-temporal resolution using environmental response functions. Agric. For. Meteorol., 232, 10-22, 2017.

Zontek, K.: Buffalo Nation: American Indian Efforts to Restore the Bison, Bison Books., 2007.

Figures

Figure 1: The study site near Gallatin Gateway, MT (45.557, -111.229). Bison locations are mapped within the 20-meter grid here superimposed in yellow. The tower location is in cyan and game camera locations are indicated in orange. Background image: Google, Maxar Technologies and the USDA Farm Service Agency ©2018.

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Table S1: The sex, age, and pregnancy status of the study bison with weight measured on November 16, 2017 shortly before they entered the pasture on November 17, 2017. Bison were assumed to be born on June 1 of the birth year by the landowners such that animals born in 2017 were nearly 6 months old when measurements began.

Sex ... [1]

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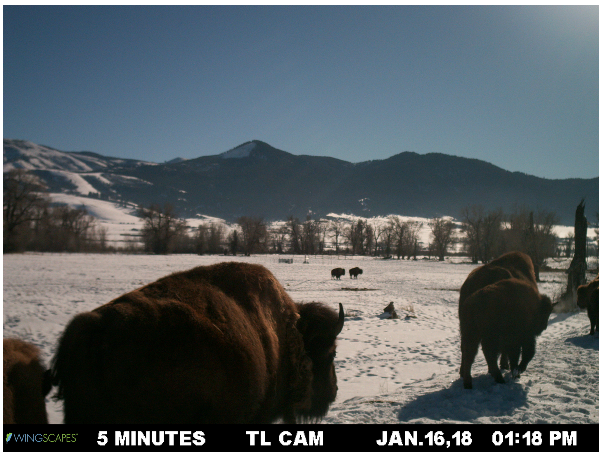


Figure 2: A sample image of bison as viewed from the south-facing time-lapse camera located to the north of the study area (Figure 1). The eddy covariance installation is visible toward the center of the study site.

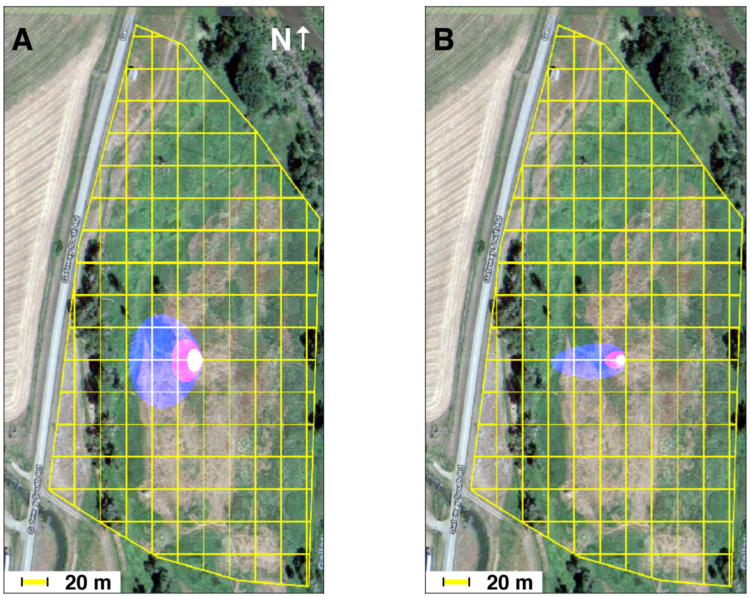
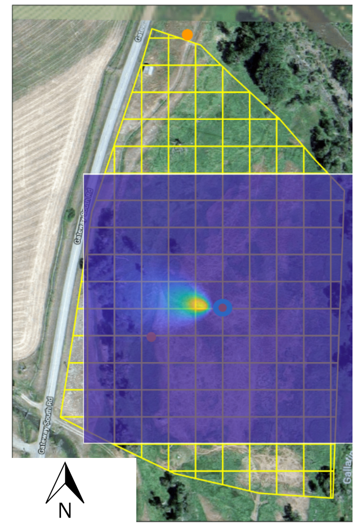


Figure 3: An eddy covariance flux footprint calculated following (A) Hsieh et al. (2000) extrapolated to two dimensions following Detto and Katul (2006) and (B) Kljun et al. (2015) for a single 30-minute interval superimposed on the study field (Figure 1). The purple, pink, and white areas represent the 95%, 75%, and 50% footprint during 1030 AM – 1100 AM Mountain Standard Time on January 8, 2018. The fraction of the footprint in each grid box is summed for each 20 m pixel to calculate the contribution of each pixel to the total flux. Background image: Google, Maxar Technologies and the USDA Farm Service Agency ©2018.



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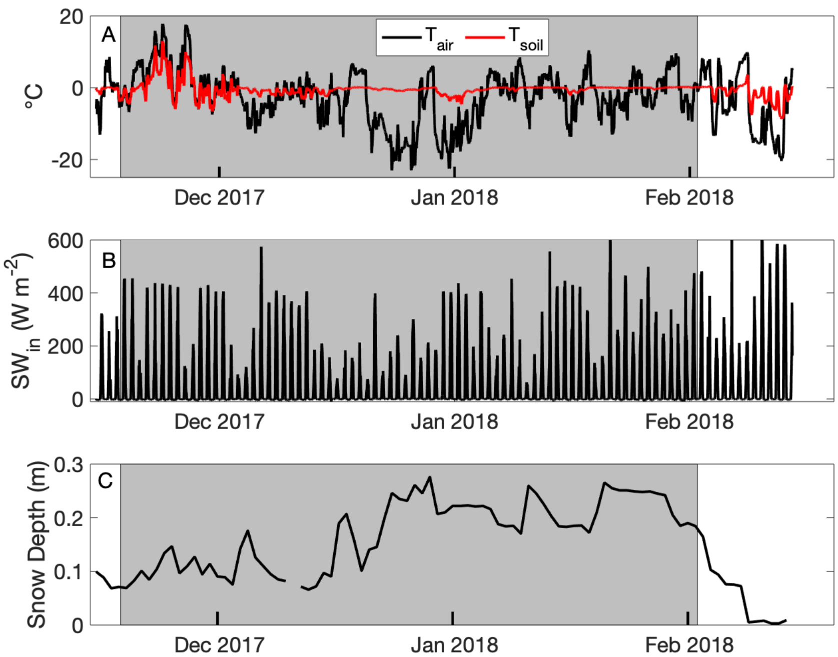

Figure 4: (A) Air (T_{air}) and soil temperature (T_{soil}), (B) incident shortwave radiation (SW_{in}), and (C) snow depth from a micrometeorological tower enclosed within an electric fence on a bison pasture near Gallatin Gateway, Montana, USA. Bison were present in the pasture during the interval bounded by the grey background.

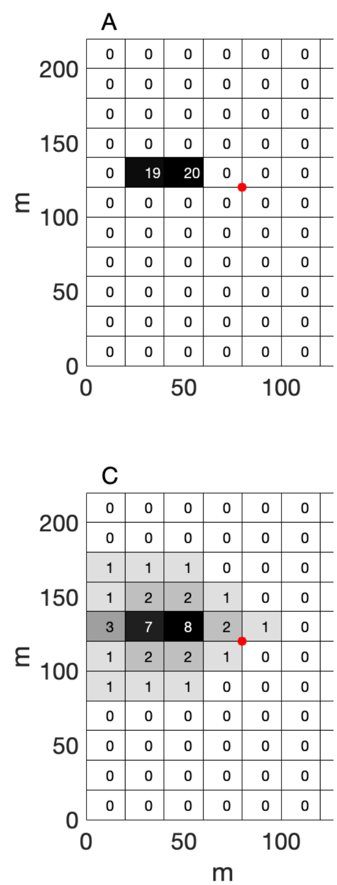

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Figure 4: The number of bison observed per grid cell at 16:30 on January 11, 2017 (A) and a distributed bison location map generated using two-dimensional Tikhonov Regularization with a Lagrange multiplier of 0.1 (B), 1 (C), and 4 (D).

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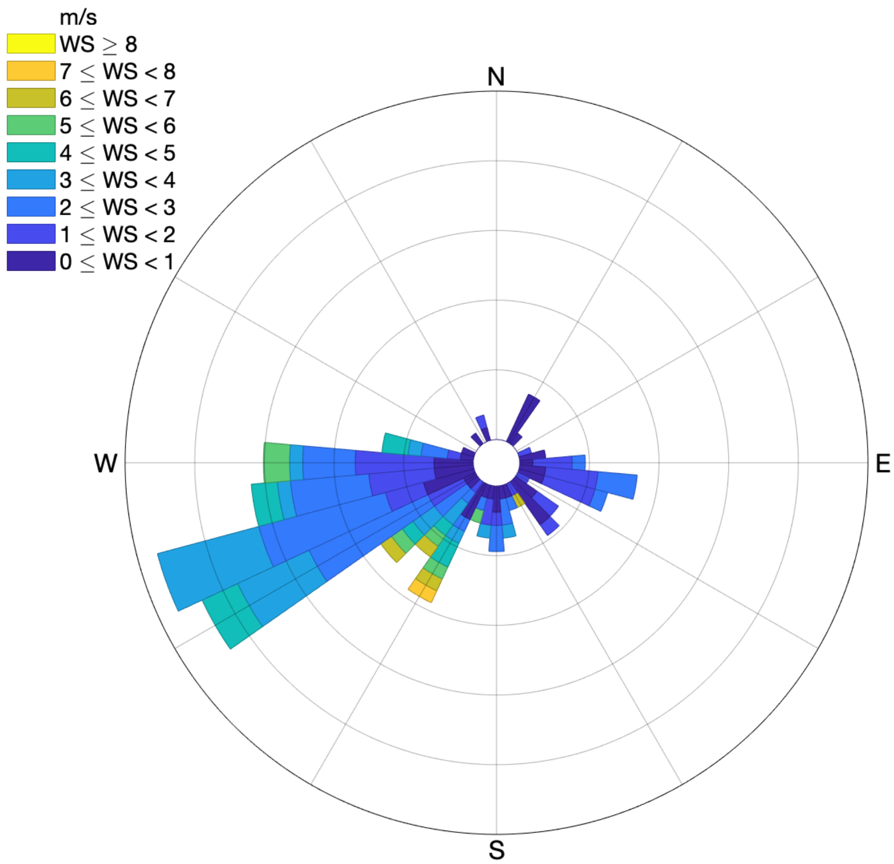

Figure 5: A wind rose following Pereira (2020) for periods when eddy covariance measurements and bison location measurements were available. WS: wind speed.

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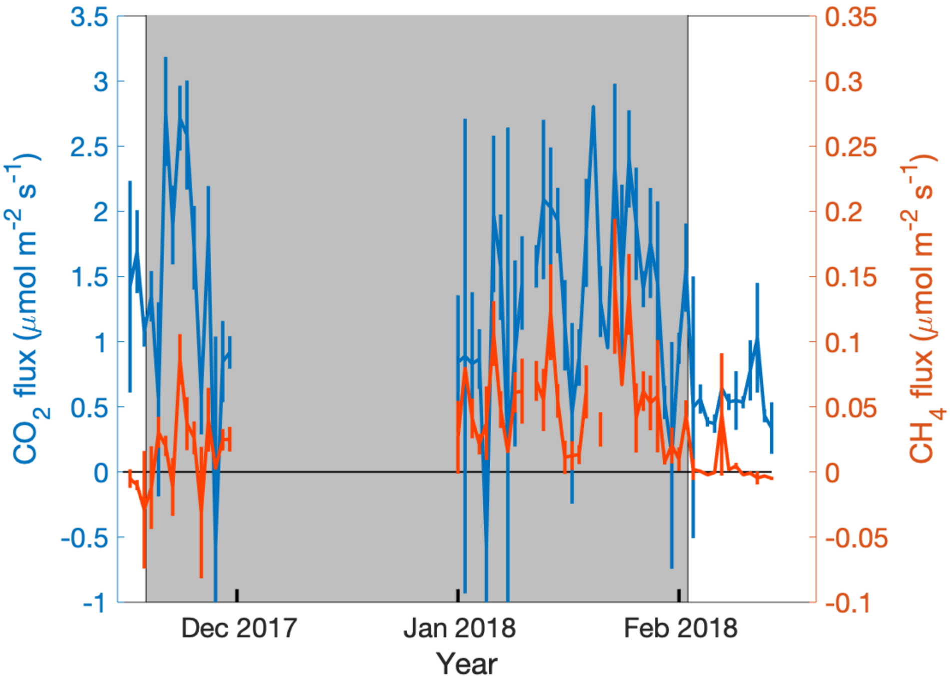

805 **Figure 6: The daily mean and standard error carbon dioxide and methane fluxes with standard error during daytime hours (0700-1700) from the study pasture near Gallatin Gateway, MT, USA. The gray background denotes the interval during which bison were present on the study site.**

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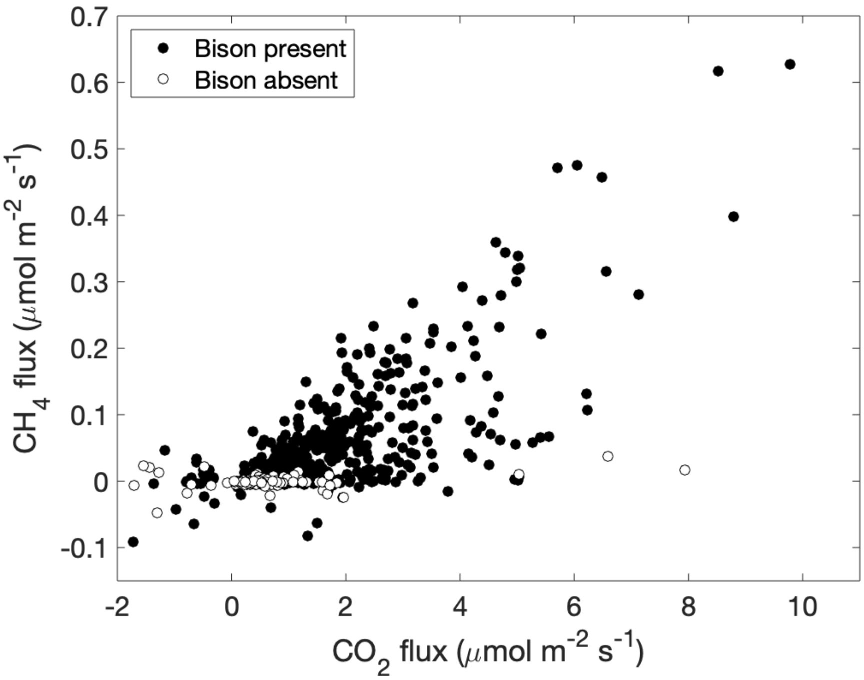

810 **Figure 7: The relationship between carbon dioxide and methane fluxes from the study pasture is shown for periods when bison were present (filled circles) and when bison were absent (open circles).**

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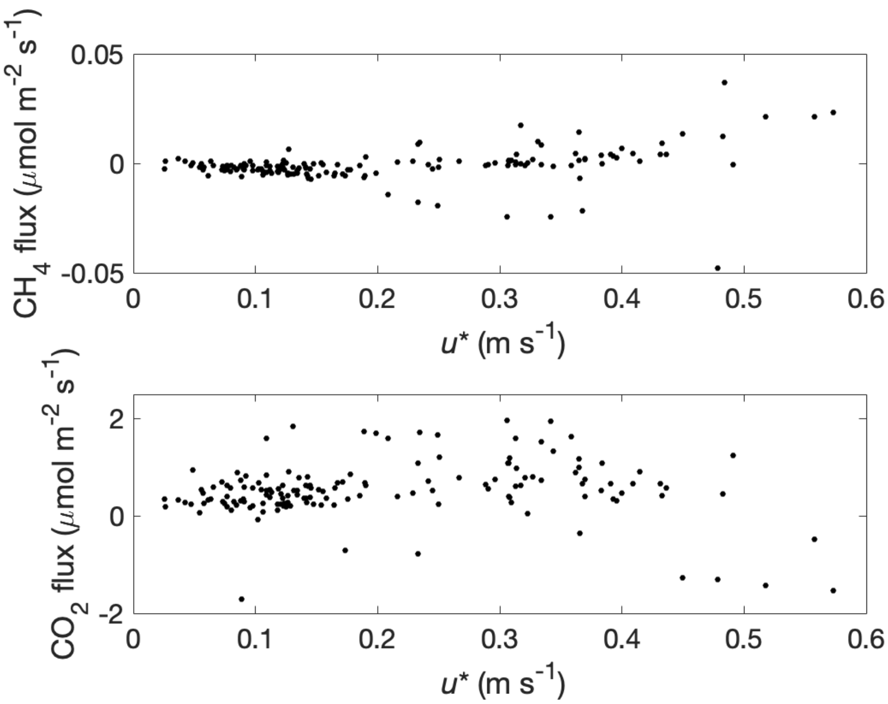

Figure 8: Methane (A) and carbon dioxide (B) fluxes as a function of friction velocity (*u) when bison were absent from the study pasture.**

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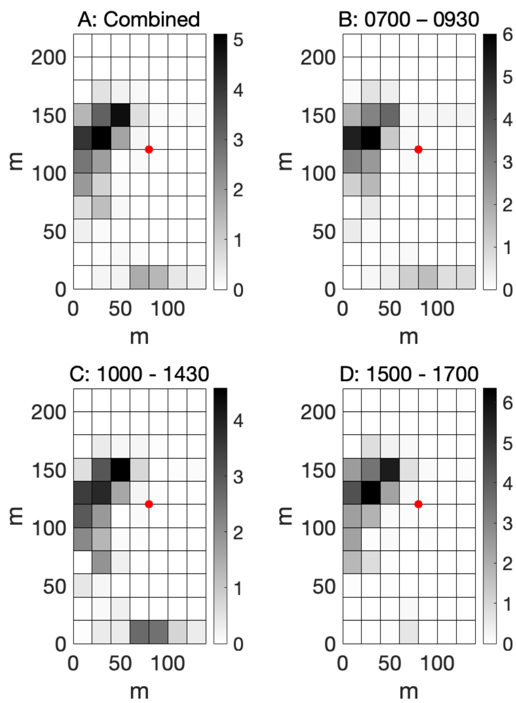

Figure 9: Average proportional bison density for three periods of the day. Each colored pixel represents a 20-meter grid square, red dots denote the location of the eddy covariance tower, and subplot titles refer to local time. Color denotes average number of bison present in each grid cell for the 39-animal herd.

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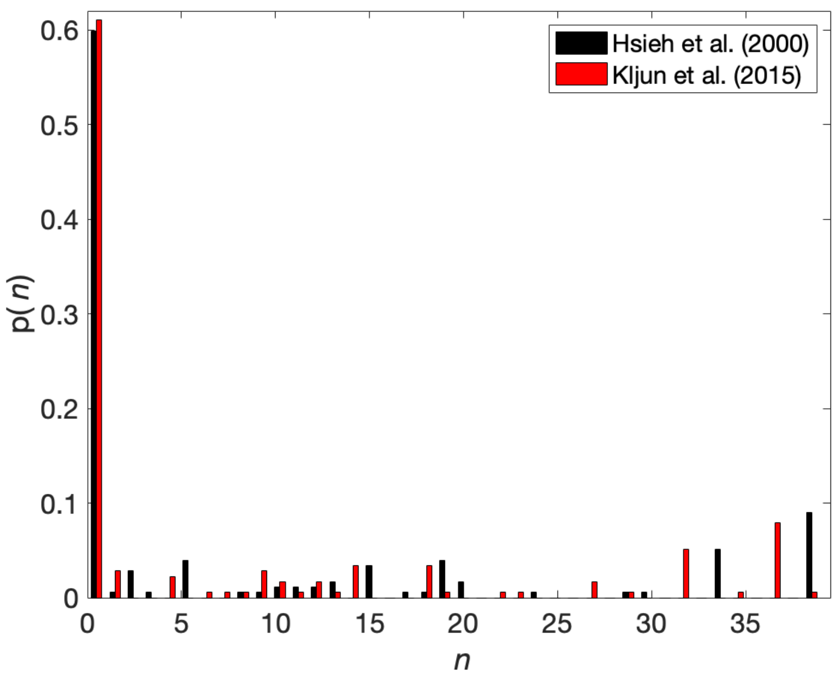

Figure 10: The probability (p(*n*)) of the number of bison (*n*) in the 90% flux footprint for the Hsieh et al. (2000) and Kljun et al. (2015) footprint models for periods when flux measurements were made and camera imagery was available.

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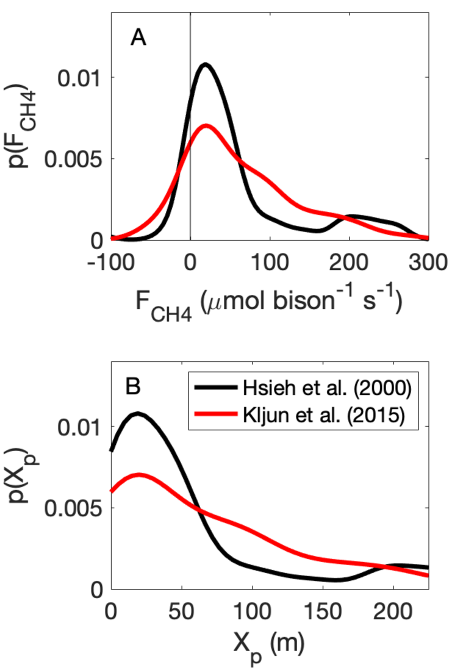

830 **Figure 11: Kernel density estimates of the distribution (p) of (A) methane efflux (F_{CH4}) on a per-bison basis and (B) the peak (X_p) of the source-weight function for half-hourly flux footprints derived by the Hsieh et al. (2000) and Kljun et al. (2015) flux footprint models.**

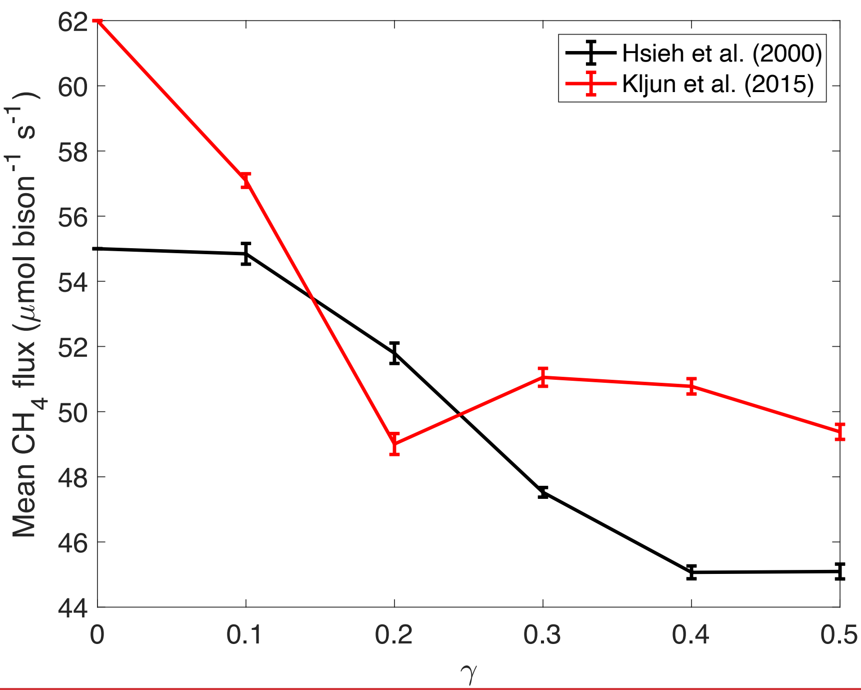

Figure 12: The estimated mean per-bison CH_4 efflux from stochastic simulations of bison locations using a probability surface defined by two-dimensional Tikhonov Regularization (see Supplemental Information) for different values of the Lagrange multiplier γ. Error bars represent standard error about the mean of twenty simulations.

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