HESS manuscript "hess-2017-47, Tree-, stand- and site-specific controls on landscape-scale patterns of transpiration" by Hassler et al.

Point-by-point response to the referee comments:

a) Response to the comments of Referee #1

Thank you very much for your very detailed and constructive comments. We address the individual points (put in italics) in the following.

1) *The paper tries to be about transpiration (starting with the title) and yet the authors explicitly state that they do not calculate transpiration because they do not have the information necessary to reliably estimate it from sap flow velocity. They cannot have it both ways. If they cannot make even a rough estimate of transpiration (or even sap flux density), then they cannot conclude anything about it, and they cannot phrase the paper as if they can. They must either make a quantitative estimate of transpiration with uncertainty (however large) and then see what they can and cannot conclude about it, or else restrict their discussion to sap velocity instead (which would be quite limiting).*

We agree that we probably used the two terms in a confusing way. We chose sap velocity as a response variable which is an equivalent to sap flux density. This was due to the reason that sap velocity was the more basic measurement variable without further assumptions about allometric relationships of diameter and sapwood area, bark thickness etc., and because the sensor installation was not always ideal in this year with outermost thermistors in some cases possibly close to the bark, so a maximum velocity is a more robust measurement than the upscaled water volume fluxes.

Additionally, we see that we could use published allometric relationships between diameter and sapwood area and a number of assumptions on bark thickness and radial variability to come up with estimations of sap flow volumes instead of velocities. However, these relationships would only tackle the tree-specific controls of the relationship between sap velocity and sap flow. In our dataset we also have the influence of the site- and stand-specific predictors. There might be ecophysiological adapations analyses which are not represented in equations based on DBH and species alone and to our knowledge there are no detailed studies incorporating these influences. Therefore, we base our primary analysees analyses on sap velocity patterns as a proxy to identify possible influences on transpiration.

Nevertheless, we agree that for being directly helpful to hydrologists – whom we primarily consider as the interested audience for our results – we should at least attempt the upscaling to sap flow, even if we can only do so with equations for tree-specific controls and the associated unknown uncertainties. We did that and repeated the multiple linear regressions for sap flow, leaving out Species, DBH and Height as they would be not be independent anymore of the target variable. We included the new Figure 8 (shown below) in the revised manuscript and added the a panel for sap flow in Fig. 9 and the respective table columns in Table 2.
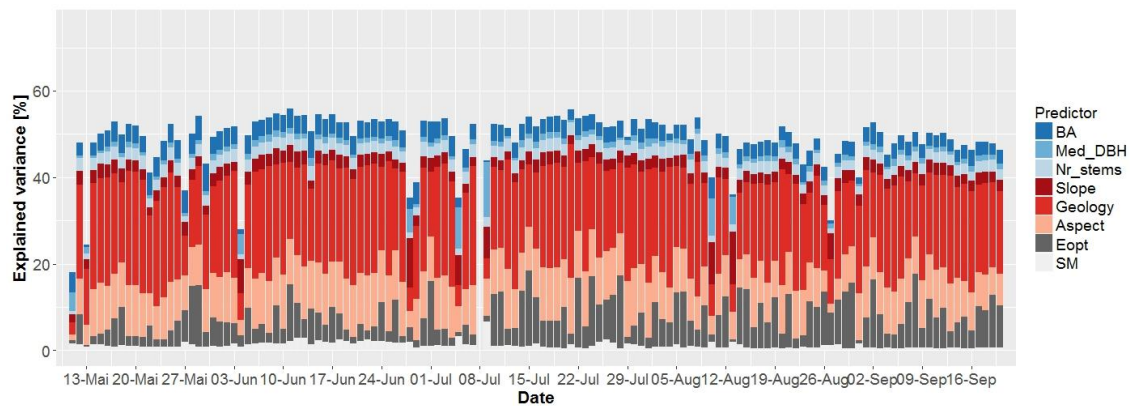
Figure 8: Proportion of variance explained by the different predictors in the daily linear models of spatial sap flow patterns: 132 daily models from 61 trees at 24 sites.

We discussed these results in comparison to those for sap velocity, adapted the method section to include the calculations for sap flow. We also included the reasoning behind why we are using sap velocity the challenges when deriving sap flow in the methods and suggestions for a way forward in the conclusions.

The individual changes are too substantial to list here, please refer to the marked-up manuscript.

2) *I think the statistical analyses do not quite get us to the reported conclusions. The authors show that a many-variable model can explain about 70% of the variability in sap velocity. But with enough variables, a model can "explain" almost any variability, without necessarily being meaningful or being able to predict variability in a new dataset. To make claims about predictive power (as the authors do), they would need to test the model's predictive power by dividing their dataset into "training data" and "testing data", as is commonly done with models. If the model successfully predicts the variability in the testing data, then a claim can be made. This approach could strengthen the paper. The focus on proportion of variability explained is also somewhat limiting and even misleading. For example, the authors highlight in the abstract that "the temporal dynamics of the explanatory power of the tree-specific characteristics, especially species, are correlated to the temporal dynamics of potential evaporation". Potential evaporation is strongly correlated with transpiration, so this finding isn't really a finding to me; it's just saying that when transpiration is small, noise dominates the variability and so the proportion of variability explained isn't a good metric to use to evaluate a model. Instead evaluating how well the fitted model can predict testing data over a range of conditions would avoid this problem.*

Obviously we did not explain well how the statistical analyses were done and what we intended with them. The purpose of the analysis was to explore if we can identify controls on spatial patterns of sap velocity as a proxy for transpiration and if these controls change over time. We do not want to find the best predictive model, but rather see this as an exploratory task, as indication, which kind of data or maps might be useful to include in spatially distributed modelling or will help in the design of regional scale monitoring networks. Nevertheless, we think this is important to keep in mind as a hydrological modeller that improving transpiration estimates in a spatially explicit way could benefit from our findings (e.g. to include information on dominant species or site characteristics which available in maps, such as geology).

We changed the paragraph about the multidimensional analysis slightly to accommodate the idea of the exploratory model exercise and comment on potential prediction two paragraphs later (changes marked in yellow):

"The multidimensional effect of all tree-, stand- and site-specific influences was then analysed with multiple linear regression models separately for each day. This modelling approach is meant to explore the main controls of sap velocity or sap flow patterns, but at this stage we do not aim at predicting these spatial patterns. The response variable…"

"Although a step-wise simplification of the models using the Akaike information criterion led to a higher percentage of explained variance by the models, we refrained from using this simplification in order to keep the model structures similar for each day to allow comparability of the temporal, day-to-day changes in predictor importance. For prediction, the potentially best model would be more appropriate, however, in our exploratory analysis we focused on comparability. The relative importance of the predictors for explaining the observed variance of sap velocity or sap flow was assessed using the approach of Grömping (2007), made available in the R package 'relaimpo'. Of the different built-in methods to determine relative importance we used 'lmg'. This method uses sequential sums of squares from the linear model, applies all possible orderings of regressors, and obtains an overall assessment by averaging over all orders, which is deemed appropriate for causal interpretation and unknown weights of the different predictors (Grömping, 2007). The initial order of the predictors in the linear models is not relevant for the relative importance as orderings are shuffled."

To make sure that our models are not overfitted, we applied a 10-fold cross-validation. We changed the respective paragraph as follows (changes in yellow) and hope it is clearer now:

"Overfitting can be a problem in linear models with many predictors. We checked for this by performing a comparison between the residual standard error (RSE) of the original models and the root mean square error (RMSE) of a 10-fold cross validation (Fig. 2). In case of overfitting, the RMSE of the cross-validation should be much higher than the RSE. In our case, both error measures differed only marginally and were largest when sap velocities were small. These were the days when the linear model generally failed to explain the variance in the datasets. For days with high sap velocities, the small errors as well as the small difference between RSE and RSME indicated that the models are not overfitted. Additionally, Figure 2 showed that limiting the analysis to the period of fully developed canopy excludes periods of larger errors at the beginning and end of the season."

We do think that looking at contributions to explained variance helps to assess the dynamics of the different influences .The overall explained variance can inform a modeller when he/she can ignore spatial patterns in transpiration estimates altogether and for example use a different model setup to focus on more relevant processes during that phase. And the differences between the Epot-dependent changes in species influence compared to the more stable influence of the site characteristics could change under different conditions such as water limitation. We elaborate some more on this in part 4.3 of the discussion.

Grömping, U., 2007. Estimators of relative importance in linear regression based on variance decomposition. American Statistician, 61(2): 139-147.

3) *The discussion is weak, tending to repeat the published literature or the present findings without addressing or even recognizing the key questions that the present findings raise. Perhaps as a consequence, the paper does not sufficiently digest the results into informative, clear conclusions, which is to say that I was left asking: what did the authors really discover? What did they want me to take away from this paper? In my view, the main candidate for a*

discovery in the present draft is the finding that several factors were all important controls on sap flow velocity but that is a somewhat vague and superficial finding, and not really a surprise, I don't think. I am sure the authors and the readers can learn more from this work. And in turn, the implications of the conclusions are not well articulated. That is, I was not convinced of why I should care about the study's conclusions. I suspect that once more substantial conclusions are expressed, then more concrete implications will follow.

Thank you for the comment, obviously the point we wanted to make with this study did not come across. We altered the introduction to better set the picture for our study in the first paragraph (please refer to the revised manuscript for that).and changed the discussion to focus better on our key findings. In our opinion these are that other than most plant-physiological studies dealing with influences on sap flow, we also examined the influence of landscape characteristics that might be relevant for hydrological modelling on the respective relevant scale. We agree that the fact that geology/soil and aspect influence sap flow is not very surprising. However, as there are no studies that actually quantify these influences compared to the well-studied tree-specific ones, this indeed is a relevant finding for better understanding transpiration variability on the landscape scale and possibly include this information in distributed hydrological models in a dynamic way. Transpiration has been identified as a major water flux that is not really well understood on a larger scale (Jasechko et al., 2013), additionally it has been shown that considering transpiration in a more detailed way can improve models greatly (eg. Seibert et al., 2017). With our studies we want to contribute to this search for better transpiration estimates. We revised the discussion and conclusions to better focus on these points.

Jasechko, S., Sharp, Z.D., Gibson, J.J., Birks, S.J., Yi, Y. and Fawcett, P.J.: Terrestrial water fluxes dominated by transpiration, Nature, Vol. 496, Issue 7445, 347-350, 2013

Seibert, S. P., Jackisch, C., Ehret, U., Pfister, L., and Zehe, E.: Unravelling abiotic and biotic controls on the seasonal water balance using data-driven dimensionless diagnostics, Hydrol. Earth Syst. Sci., 21, 2817-2841, https://doi.org/10.5194/hess-21-2817-2017, 2017.

4) *The writing is good but the ideas could be made easier to follow. For example, it's hard to wrap one's head around a heading like "Temporal dynamics of predictor importance for explaining the daily spatial sap velocity patterns". This heading refers to the dynamics of a statistic that is itself a summary of dynamics. Moreover, "for explaining the" adds confusion because it is largely redundant with "predictor", and the term "daily spatial sap velocity patterns" is an ambiguous way to condense "spatial patterns in daily mean sap velocity" that is, if I have understood the authors' intended meaning correctly. So this is a section about temporal patterns in the ability of the model to predict spatial patterns in a temporal average of sap velocity. That is quite a convoluted idea. Is it really the best way to look at the data? If so, great care must be taken to guide the reader through it.*

Thank you for pointing this out. The heading is probably easier to understand if it is simply called "Temporal dynamics of predictor importance". As we talk about the linear models at length before, it should be clear which predictors are meant and further explanation follows in the text. We changed both headings, in the results and discussions section. Similarly we were happy to change the occurrences of "daily spatial sap velocity patterns" to "spatial patterns in daily mean sap velocity", thanks for the suggestion. Of course we cannot be sure if we chose the best way to look at the data, but taking a sap velocity average per day and looking at variance contributions

of linear model predictors seems to be an appropriate way to both analyse the spatial patterns and the temporal dynamics of predictor importance. We also repeated these analyses now for sap flow and compared the results.

We asked test-readers to check if the methodology and results are phrased in an understandable way and changed the wording according to their suggestions.

SPECIFIC COMMENTS

We were happy to adopt the minor technical comments about paragraphs and wording you put into the supplement pdf and also changed the type in Fig. 6. Thank you for making this effort.

p1, l28: Soil only affects transpiration via plant-physiological characteristics. It also seems strange to single out soil but not the atmosphere here.

We wanted to list the "resistance" terms here. In this sense we consider the atmosphere as the main driver for transpiration and water supply - directly linked to groundwater resources, rainfall amounts etc. - as the boundary conditions of the process. But on top of that the transport capacity of the plants and the soil (to a degree of course also hydraulic properties of aquifers…) shape the actual flux. We think this sentence is clear enough and actually kept it with some minor changes.:
"The main controls of this water flux in vegetated ecosystems are plant-physiological and soil characteristics."

p2, l33-5: As stated, this doesn't make sense to me. If canopy transpiration was varying due to length of the growing season, then the effect would surely be seen in the sap flux densities of individual trees, which are also affected by the growing season length. Perhaps the contrast was between total annual transpiration and instantaneous summertime transpiration, rather than between tree and canopy scales?

The comparison is actually between both, temporal and tree-canopy scales. One of their main results is that total annual canopy transpiration shows an elevation effect due to growing season length. As they also compare sap flux densities of individual trees, we also report this result because it is more comparable to our study. We will clarify the sentence as follows:
"Maximum sap flux density of individual trees during clear-sky days, however, did not vary significantly due to these effect."

p3, l1-6: This paragraph seems out of place. It reads like you're moving on to a new topic, but in fact you are reiterating the idea of site-specific characteristics influencing sap flow, which you were talking about on the previous page.

The paragraph was meant as a short summary of the main points in the introduction to lead to our goals of the study. We know that it is repetitive but kept it to get the idea across why we did the study in the first place. We add a "to summarize" in front to make clear that it is not a new topic and follow up with our goals for the study in the next paragraph.

p4, l39: The driving gradient for transpiration is often phrased as an aspect of atmospheric conditions, as here, but in fact, what's more important than the atmospheric water vapor pressure (i.e. the end of the vapor pressure gradient, which typically doesn't vary much over the course of the day) is the temperature of the leaves and associated saturation vapor pressure therein (i.e. the start of the vapor pressure gradient, which varies a lot from day to night and is the reason why transpiration is typically

negligible at night). So it would probably be most accurate to say that the main environmental limitation to transpiration (and therefore sap flow) is the solar heating of the leaves.

We were happy to change the sentence to "The main environmental limitations to sap flow are the atmospheric conditions (the solar heating of the leaves, water vapour pressure deficit, etc.) as the driving gradient for transpiration and the water supply to the trees." to be more specific here.

p5, l34-6: This seems backwards. Slopes less than 5 degrees, called "Plain" would be a category in aspect, not in slope position; and less steep parts of slopes would be a category in slope position, not aspect.

We struggled with the nomenclature for these categories for a while and kept renaming them. Maybe the easiest way to avoid confusion here is to call the "plain" in aspect "no-aspect" and the "flat" in slope "no-slope". We changed the revised manuscript accordingly.

p6, l34-5: I am not familiar with this method, and so I do not understand the idea here or the meaning of Fig. 2. Please provide at least a reference to let unfamiliar readers understand what you are doing here.

We elaborated this a little bit more in the methods section (see the text block regarding overfitting which we added to your general comment 2 above). We hope it is clearer now.

p7, l8-9: This result confirms what I said in my comment above: the most important control on sap velocity is solar heating of the leaves (the only real variable in your E_pot equation is solar input).

Yes, solar input is the main variable to Epot, however, this measure is also comparable to the Penman-Monteith approach, and the original study by Renner et al. (2016) also tested for additional effects of vapor pressure deficit and wind speed on transpiration and the results did not show a distinct effect. Nevertheless, we don't have measurements of leaf temperatures so we could only speculate, which process is most important. Epot seems to be a robust measure which is appropriate to the measurement data of the atmospheric variables we have available in our research area so we use it as an approximation of evaporative atmospheric demand. We added two sentences to the methods paragraph 2.3 to make clear why we use this measure.

Renner, M., Hassler, S.K., Blume, T., Weiler, M., Hildebrandt, A., Guderle, M., Schymanski, S.J. and Kleidon, A., 2016. Dominant controls of transpiration along a hillslope transect inferred from ecohydrological measurements and thermodynamic limits. Hydrology and Earth System Sciences, 20: 2063-2083.

p7, l31: The "few days" look like 2 months to me.

We changed the sentence to "In contrast, there were only 36 of the 132 days showing significant differences for geology and 25 days for slope position, occurring when sap velocities were generally low." to emphasise which difference we mean here.

p8, l21: I could not figure out what you meant by this until I looked at the figure. It was not clear what was being cumulated, which variance you were talking about, or what the contributions were to. Statistical analyses often involve technical details and jargon that make them difficult for the average reader to follow unless extra care is taken to describe them clearly (at the expense of brevity). For example, you might refer to "the proportion of variance explained by all the tree-specific predictors taken together, all the stand-specific predictors taken together, and all the site-specific predictors taken together".

Thanks for helping to simplify this. We happily adopted your phrase instead of our more complicated one.

p8, l22-4: I actually have the impression that if you scaled the site- and stand-specific lines up to have the same mean as the tree-specific line, then all the lines would be seen to vary similarly.

According to your suggestion, we compiled the following figure (by subtracting the mean and dividing by (max-mean) for each time series) and also calculated Spearman rank correlations.
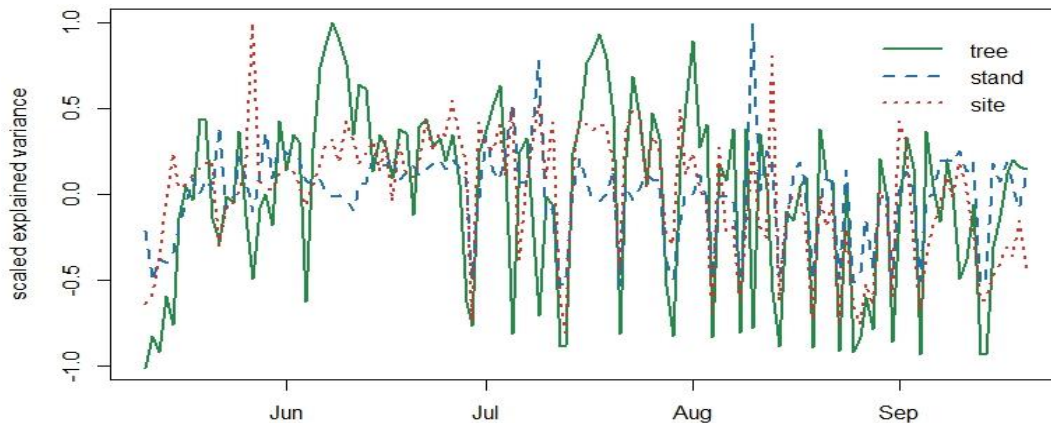
Response Figure 1: Scaled explained variance of tree-, stand- and site-specific predictors.

Some of the variations indeed occur in all three lines, however we think it is appropriate to state that the tree-specific line varies more than the others. Rank correlations are all significant, however not very strong (rho = 0.31 between tree and stand, 0.58 between tree and site, 0.42 between stand and site). Looking at the absolute variability of the lines in the new Figure 9 and the correlations of both "Species" and "tree-specific" explained variance to Epot we kept our original line of reasoning here.

p9, l23-31: This is really just restatement of results. You are missing the opportunity for discussion and analysis here. For example, you repeat the observation that Epot doesn't explain much spatial variation but fail to connect the dots and say that it's not surprising that Epot drives temporal variation but not spatial variation given that Epot itself varies a lot temporally but not so much spatially.

You are right, there was room for improvement in the discussion. We happily took up your suggestion and condensed more what our results actually mean. Please refer to the revised manuscript; the discussion has changed quite a bit.

p9, l31-5: Here you are getting into discussion, but I think you are missing the real point because you are writing as if your measurements were of transpiration or sap flux density instead of sap velocity. Of course big trees will transpire more, but they also have bigger trunks with more sap "bandwidth". A question that I think you should be asking here, and to which your data might speak, is how transpiration and sap velocity scale with tree size. That relates to allometry: how does the canopy size scale with DBH and sap "bandwidth"?

As you already stated in your very first comment, one main issue we had to clarify in this manuscript was the distinction between sap velocity and sap flow. In the revised version the linear models and the following analyses were done for both sap velocity and sap flow and the discussion consequently includes the comparison now.

p9, l36: Was this a statistically significant effect?

The average explained variance of 4 % for stand density resulting from the analysis of the predictors' relative importance indicates that there is an effect of stand density, albeit a small one. A test of significance within the relaimpo package would require a bootstrapping procedure which is not available for models that also contain factors as predictors. If you would suggest a straightforward method with which we might test significance, we will happily apply it and provide the details in the revised version of the manuscript. However, we suspect your main concern here is with the relatively small effect of only 4%. We agree that we should not over-interpret this result and changed the wording accordingly.

p9, l37-8: You are glossing over the difference between sap velocity and sap flux (or transpiration) here. I do not think you should conflate them; rather I think you should use the discussion to explicitly consider how they might relate.

In the revised version of the manuscript we also included sap flow and discussed the differences in more detail accordingly.

p10, l12-6: Here I feel like I am reading the same few points from the literature over and over, slightly rephrased: e.g. water availability depends on the type of ground. I knew that before reading your article. What I am looking for as a reader of your discussion is to learn something from your findings. How do these points from the literature help me learn something from your findings?

The main point we want to convey in our manuscript is that hydrologists applying spatially distributed models or otherwise interested in transpiration patterns at the landscape scale could benefit from considering aspect and geology as influencing factors in addition to the physiological properties of trees and stand composition and characteristics. We agree that this did not really come across in this paragraph and rewrote the discussion to form the link to the implications for hydrological modellers in the revised manuscript.

p10, l17-8: This is, at first glance at least, very surprising and contradicts the positive temporal correlation of Epot and sap velocity. You should comment on that. The sampling effect of oak vs beech is something it seems you could (and should) check statistically with your data.

Looking at the temporal and spatial variability of Epot this is not very surprising, as the former is much higher than the latter. But you are right, we should have mention that in the manuscript, we did so in the revised version. The differences in sap velocity if grouped according to species and aspect is shown in the following figure.
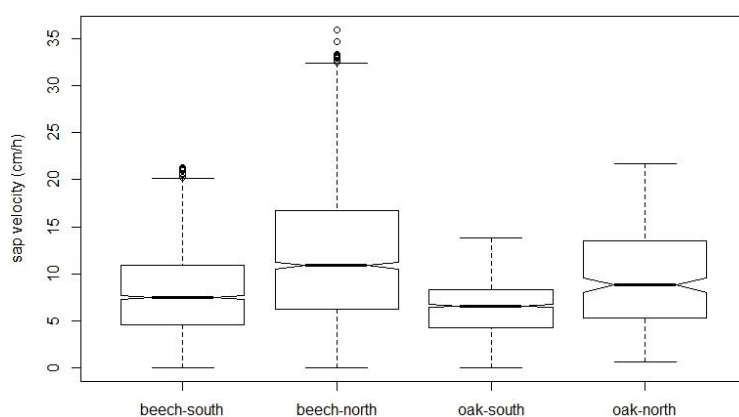
Response Figure 2: Sap velocities if grouped according to species and aspect.

Within the same species the aspect difference is still present and significant according to Welch's two-sample t test, so we are quite confident that we don't have a problem due to the sampling effect for species and removed the comment in the manuscript.

p10, l33-4: The key point that I have not seen you address is how much the drivers themselves vary. That is surely the reason why Epot doesn't have much spatial explanatory power, as I noted above. I wonder whether the explanatory power of each predictor just depends on how much that predictor actually varies.

I'm not really sure if we understand you correctly here. But what we are interested in is indeed the influence of the difference predictors in a landscape on sap velocity patterns. If the predictors vary a lot spatially and thereby affect sap velocity or sap flow, the more reason to include them into transpiration estimates, because Epot (or other measures of potential evaporation) alone would not be able to reflect these patterns. As we re-wrote large parts of the discussion, we hope this became clearer now.

p10, l34-40: Again, this paragraph is mostly just repeating findings. In a discussion, I'm looking for the "why?", at least some informative speculation. The fact that species explains a lot of spatial variation on some days and little spatial variation on other days was surprising to me. Why is that? Is it that conditions on some days are favorable to all species while conditions on other days favor one species over another?

We tried to explain the species effect in the last sentence of that paragraph. If beech trees can respond to higher Epot with higher sap velocities and oaks only respond to a certain threshold, especially high-Epot days will lead to larger species contrasts. We did not add any more explanation about the species differences at this point, but instead added more discussion on the species contrast in section 4.2.

p11, l3-4: It sounds like you're saying that when Epot is low, there isn't much sap velocity, and the variability in sap velocity is just noise. That is probably true, and it is a reason why proportion of explained variance alone is not a great way to assess the effect of a potential predictor on sap velocity.

We disagree on this point. We think that explained variance is an appropriate measure for our purpose. However, you are right that we can't say much about days when the linear models completely fail to explain the spatial variability in sap velocity. These days should not be interpreted. We think the relation of total explained variance and Epot is still interesting though because it shows when the environmental conditions equalize the spatial contrasts, therefore we do not exclude days of little explained variance completely. But we calculated the mean variance contributions of the predictors also when excluding days with less than 40 or 45 % total explained variance and the general pattern stays the same, so we refrained from opening up that comparison. For modellers attempting a temporally dynamic model setup, information when to include spatial detail for which process is relevant. We referred to this in the last part of the discussion 4.3.

p11, l9-17: This kind of discussion needs to happen earlier, as each topic is discussed.

As we included the models for sap flow in the revised manuscript, this discussion indeed is happening earlier now.

b) Response to the comments of Referee #2

Thank you very much for your detailed comments. We address the individual points (put in italics) in the following.

The main results are that hydrometeorological conditions (evaporative demand and soil water supply) explain little variation in landscape-level sap flux patterns, compared to that explained by site-, stand- and tree-level factors.

It seems that our main point came not across clearly. Our main result is not that the hydrometeorological conditions do not explain much of the spatial patterns, but that apart from the obvious tree-specific predictors, the sites-specific predictors actually explain a considerable part. This is of interest for hydrological modellers trying to improve spatially explicit transpiration estimates. We adapted the first paragraph of the introduction, discussion and conclusions to make that clearer, please refer to the revised manuscript.

First, the authors present sap velocity (probably better named as sap flux or sap flow density, per unit sapwood area) not tree transpiration. While sapwood area-based sap flow density may be an interesting quantity in itself for more physiologically-oriented studies, where water transport characteristics are compared across species or ecological settings, it may have less interest from the hydrological point of view. A more natural approach would be to scale sap flux to whole-tree sap flow, using tree sapwood area and a reasonable integration of spatial variation of sap flux within the sapwood.

Thank you for the comment. This point was also made by referee #1, so this is a copy of the response to that comment.

We chose sap velocity as a response variable which is an equivalent to sap flux density. This was due to the reason that sap velocity was the more basic measurement variable without further assumptions about allometric relationships of diameter and sapwood area, bark thickness etc., and because the sensor installation was not always ideal in this year with outermost thermistors in some cases possibly close to the bark, so a maximum velocity is a more robust measurement than the upscaled water volume fluxes.

Additionally, we see that we could use published allometric relationships between diameter and sapwood area and a number of assumptions on bark thickness and radial variability to come up with estimations of sap flow volumes instead of velocities. However, these relationships would only tackle the tree-specific controls of the relationship between sap velocity and sap flow. In our dataset we also have the influence of the site- and stand-specific predictors. There might be ecophysiological adapations which are not represented in equations based on DBH and species alone and to our knowledge there are no detailed studies incorporating these influences. Therefore, we base our primary analysees analyses on sap velocity patterns as a proxy to identify possible influences on transpiration.

Nevertheless, we agree that for being directly helpful to hydrologists – whom we primarily consider as the interested audience for our results – we should at least attempt the upscaling to sap flow, even if we can only do so with equations for tree-specific controls and the associated unknown uncertainties. We did that and repeated the multiple linear regressions for sap flow, leaving out Species, DBH and Height as they would be not be independent anymore of the target variable. We included the new Figure 8 (shown below) in the revised manuscript and added the a panel for sap flow in Fig. 9 and the respective table columns in Table 2.
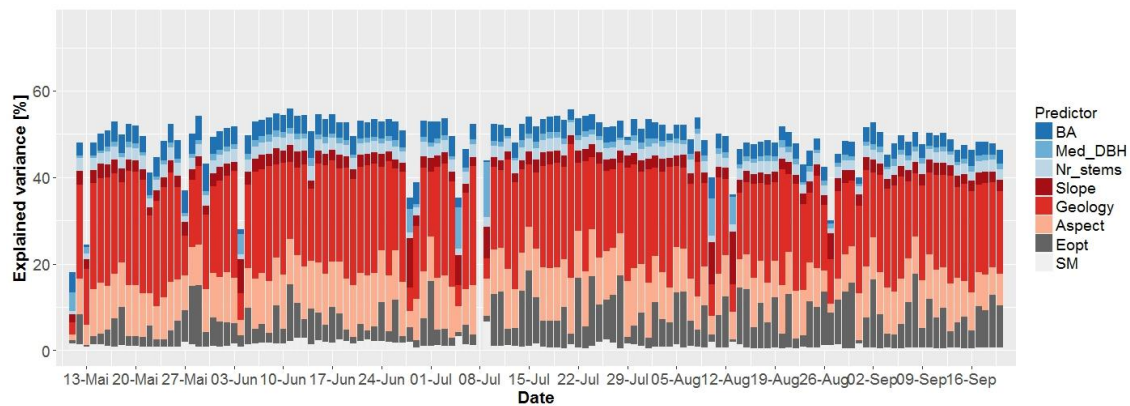
Figure 8: Proportion of variance explained by the different predictors in the daily linear models of spatial sap flow patterns: 132 daily models from 61 trees at 24 sites.

We discussed these results in comparison to those for sap velocity, adapted the method section to include the calculations for sap flow. We also included the reasoning behind why we are using sap velocity the challenges when deriving sap flow in the methods and suggestions for a way forward in the conclusions.

The individual changes are too substantial to list here, please refer to the marked-up manuscript.

A related point is that, even if sensors measuring sap flux in three points along the tree's xylem depth were installed, so potentially accounting for some of the radial variation in sap flux, the authors chose only the point with the highest sap flux values (pg. 4, L. 33). In my opinion, they should integrate sap flux over the probe length and make some assumption about the variation of sap flux beyond the probe length and up to the sapwood-heartwood boundary.

Our main reason for selecting the maximum sap velocity of the three velocities we can obtain from the sensors' profiles was to have a robust estimate of sap velocity. As stated above, sensor installation was not always ideal in this year, so the maximum sap velocity seems the most reliable measure of something like a transpiration potential. Therefore we based our primary analyses on this measure – ignoring that depending on the sapwood depth we will have different sap flow rates.

Nevertheless we agree that a tentative upscaling and looking at the models of sap flow is helpful, when the uncertainties associated with the upscaling are kept in mind. We stated how we incorporated this in the response to the comment above. We adapted the discussion accordingly to also address the differences between the results about sap velocity and sap flow.

As for the modelling approach, I think that the contribution to explained variation by the different the predictors, will depend on the order in which these predictors are introduced in the model, something that is not stated in the methods. In other words, do results of the variable importance analysis change if hydrometeorological variables are introduced first, and then the rest of the factors?

You are right, if we were to simplify the models so that we had only the best for each day, the order of the predictors would be important and also the contributions would change slightly. In our case the order of the predictors is not important because the variable importance assessment calculates a mean of all possible orderings. We revised this part (last paragraph on page 6 in the original manuscript) follows and hope it is clearer now (changes in yellow):

"Although a step-wise simplification of the models using the Akaike information criterion led to a higher percentage of explained variance by the models, we refrained from using this simplification in

order to keep the model structures similar for each day to allow comparability of the temporal, day-to-day changes in predictor importance. For prediction, the potentially best model would be more appropriate, however, in our exploratory analysis we focused on comparability. The relative importance of the predictors for explaining the observed variance of sap velocity or sap flow was assessed using the approach of Grömping (2007), made available in the R package 'relaimpo'. Of the different built-in methods to determine relative importance we used 'lmg'. This method uses sequential sums of squares from the linear model, applies all possible orderings of regressors, and obtains an overall assessment by averaging over all orders, which is deemed appropriate for causal interpretation and unknown weights of the different predictors (Grömping, 2007). The initial order of the predictors in the linear models is not relevant for the relative importance as orderings are shuffled."

Grömping, U., 2007. Estimators of relative importance in linear regression based on variance decomposition. American Statistician, 61(2): 139-147.

Also related to the models, the authors focus on the variance explained by the different predictors but they do not go into much depth in the direction of change in sap flux with the variation in the predictors (which is necessarily complex given the multiple variables involved).

We agree we do not go into much depth concerning the single-factor analyses. But as we know that we have a multivariate problem, we do not want to over-interpret these relations, but rather give a first general overview of the data in Fig. 4 which can give some indication of the univariate response. But we focus our main analyses on the multivariate approach using the linear models.

The presentation of the results could also be improved. For instance, Fig. 4 could focus only on the most important variables (reduce the number of panels) and use conditioning symbols, shapes or colours to show multivariate relationships; one example, sap flux density vs dbh coded by species, geology or basal area categories.

This comment relates to the one before. We do not want to over-interpret univariate graphs, but give a data overview. Therefore we also think that having all panels in the figure is more informative than pre-selecting and further interpreting relations based on three-variate plots. After all that is why we chose to use the multiple linear regression as an analysis tool. However, as the discussion is now considerably revised, the sap velocity and sap flow contrasts due to the different predictors is more elaborated there.

Overall, the study does not seem to convey a clear message or a novel result. Some of the findings on the structural controls of sap flow across the landscape are not really that new (Adelman et al. 2008, Loranty et al., 2008, Angstmann et al. 2013, Tromp-van Meerveld & McDonnell, 2006, the last two studies cited in the manuscript).

We agree that the message could be clearer and are confident that we managed to do so in the revised manuscript. However, we do think we show a novel result. After all, there are only very few studies which actually compare the multiple influences on transpiration that exist in a landscape experimentally and try to quantify their importance to better inform spatially explicit transpiration estimates which could be used for example by modellers. Previous studies mostly considered only one additional factor to the well-studied tree-specific ones.

Thank you for suggesting the two studies, we included them in the introduction. However, they also do not provide a more general attempt at identifying the most important influences on transpiration patterns in our landscape. Adelman et al. (2008) suspect an effect of differences in water availability on a slope due to contrasts in species composition, but did not see the effect of slope position on

transpiration, possibly because it was too late in the season and therefore to dry over the whole slope. And Loranty et al. (2008) find that species spatial patterns mainly control spatial patterns of transpiration, but did not see dependence of sap flux density on a moisture gradient along a slope. However, they also state that soil moisture was possibly not limiting for transpiration in their study because it was overall wet enough and, for example, the studied aspen is quite drought-tolerant.

Altogether we see the dire need for more studies on the topic of influences on transpiration at the landscape scale, in different landscape settings, with different species, at best also with experiments targeting univariate effects, and last but not least with independent transpiration estimates (which would need measurements of sapwood area and its properties for each tree) to test the hypotheses. Especially if hydrologists want to go beyond using the Penman-Monteith equations in spatially explicit models to improve spatial representation of transpiration, estimates on influences that could be obtained from maps would help to improve models. We revised the introduction, discussion and conclusions to accommodate these thoughts, implications and novelty of our study.

Adelman, J.D., Ewers, B.E. and MacKay, D.S., 2008. Use of temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration. Tree physiology, 28, 647.

Loranty, M.M., Mackay, D.S., Ewers, B.E., Adelman, J.D. and Kruger, E.L., 2008. Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient. Water Resour. Res., 44.

Specific comments

P. 5., L. 6. What about the role of vapour pressure deficit in driving transpiration? Epot here seems to include a radiative term only.

Concerning the role of vapour pressure (VPD) deficit: In an earlier version of the study we looked at temperature, radiation and VPD separately. However, we were reminded that a combined measure of atmospheric evaporative demand would be more suitable and we agree with that. The proposed measure by Renner et al (2016) is somewhat comparable to a Penman-Monteith approach, albeit based on thermodynamic principles. The simplicity of the equation and the necessity of only shortwave radiation makes it easier to use with the available measurements in the study area. In their paper Renner et al. (2016) tested for additional effects of VPD and wind speed on transpiration and the results did not show a distinct effect. These tests and the shown comparability, although slight underestimation, to Penman-Monteith suggests it is a good way of assessing evaporative demand for our purpose. We added two sentences to the methods paragraph 2.3 to make clear why we use this measure.

Renner, M., Hassler, S.K., Blume, T., Weiler, M., Hildebrandt, A., Guderle, M., Schymanski, S.J. and Kleidon, A., 2016. Dominant controls of transpiration along a hillslope transect inferred from ecohydrological measurements and thermodynamic limits. Hydrology and Earth System Sciences, 20: 2063-2083.

p. 7, L. 16 - 22. Please see my comment above on the possibility of showing bivariate plots with conditioning variables to show interactions between predictors.

We understood the comment above as a suggestion to show univariate response plots for sap velocity conditioned with a second predictor variable. This comment then refers to generally showing interrelations between predictors. We did not to that in this study but described it when explaining the preparations for the modelling in the methods sections. We believe this sufficient and showing x-

y-Plots of all predictor pairs would not contribute a lot to the focus of the study. However, if desired we can put the x-y-Plots in an appendix.

P. 9, L. 2 - 18. I don't fully agree with the explanation that soil moisture limitations are not detected because soil water availability is not exhaustively measured (over the entire soil profile or taking into account water in fractures). Transpiration shows a threshold response with declining soil moisture, and even when deeper soil layers may be playing a role in supplying water you could still detect a (highly non-linear) relationship with most soi layers (e.g. Duursma et al 2008). Even if water was taken from deep layers, transpiration would still be related to soil water status in the upper layers (Warren et al., 2004).

Thanks for pointing this out. We don't claim to have the true explanation for the lack of detected soil moisture limitations. One possibility would be that high moisture contents on rainy days with low transpiration are causing this effect. We checked on this by redoing the correlation analyses while excluding rainy days.
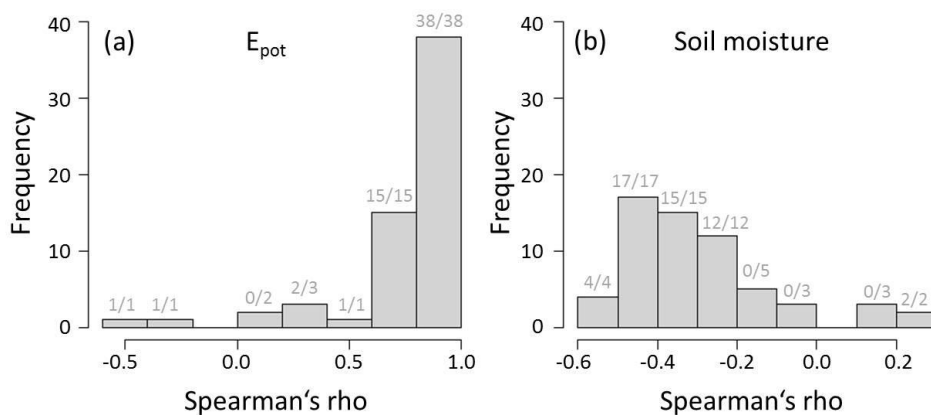
Response Figure 3: Histograms of temporal correlations between (a) E_{pot} and (b) soil moisture at each site with sap velocity for the 61 trees in the dataset, **while excluding days with more than 0.1 mm rainfall**, based on official measurement stations in Useldange and Roodt. The small numbers in grey on top of the bars indicate how many of the correlations in the specific group are significant.

The histograms did not change markedly, so we do not think that the rainy days contort the correlations here. So we still consider the argument that soil moisture in the top 50 cm is not a good proxy for water availability as most likely and stick with this in the discussion.

P. 10, L. 31-34. There are indeed some studies on this; see the Adelman et al 2008 study cited above on the spatial patterns of physiological regulation of transpiration. P. 10, L. 39-40. Could this lack of sensitivity for oak be caused by the inherent limitations of the heat ratio method in measuring high flows (see e.g. Vandegehuchte & Steppe, 2013).

Indeed there are some studies about spatial patterns of transpiration (albeit not many), but rather from a plant physiological point of view than from a hydrological one. As we are discussing the temporal dynamics of predictor importance in this paragraph we are referring to the dynamics of the multivariate predictors' effects which to our knowledge has not been studied at all so far. Maybe it makes things clearer if we put "multivariate controls in a landscape" instead of only "controls" in line 34.

We don't really see how a lack of sensitivity for oaks can be a sensor limitation as the sap velocities of the beech trees are generally higher than the oaks anyways. Did we misunderstand your comment here?

P. 11, L. 5-15. The authors should try to upscale sap flow density to sap flow using the three measuring points along the sapwood and using sapwood areas (measured or derived from allometry). Although they would need to make some assumptions on the circumferential variability, but nevertheless, I think it's worth doing the scaling.

We do have our reservations about using published allometric relation that are based on only the tree-specific influences, however, as stated above, we included the linear models based on sap flow in the revised version of the manuscript for comparison and discussed the differences.

P. 11, L. 11-12. Other studies show sap flow well beyond the outermost ring in deciduous oaks (e.g. Poyatos et al., 2007).

Yes, we agree that oaks transpire not only in the outermost ring, we tried to stress this by putting the word "annuli" instead of "annulus" in the text of the original manuscript. But furthermore, the main interest here is the comparison to beech trees and they reportedly transpire up to greater depths (eg. measured 6-8 cm and estimated 10-12 cm in Gebauer et al. ,2008). This part of the discussion was moved to 4.2 in the revised manuscript and we hope we made it clearer now.

Gebauer, T., Horna, V. and Leuschner, C., 2008. Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species. Tree physiology, 28: 1821-1830.

Tree-, stand- and site-specific controls on landscape-scale patterns of transpiration

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Abstract. Transpiration is a key process in the hydrological cycle and a sound understanding and quantification of transpiration and its spatial variability is essential for management decisions as well as for improving the parameterisation
10 and evaluation of hydrological and soil-vegetation-atmosphere transfer models. For individual trees, transpiration is commonly estimated by measuring sap flow. Besides evaporative demand and water availability, tree-specific characteristics such as species, size or social status control sap flow amounts of individual trees. Within forest stands, properties such as species composition, basal area or stand density additionally affect sap flow, for example via competition mechanisms. Finally, sap flow patterns might also be influenced by landscape-scale characteristics such as geology and soils, slope
15 position or aspect because they affect water and energy availability; however, little is known about the dynamic interplay of these controls.

    We studied the relative importance of various tree-, stand- and site-specific characteristics with multiple linear regression models to explain the variability of sap velocity measurements in 61 beech and oak trees, located at 24 sites spread over a 290 km²-catchment in Luxembourg. For each of 132 consecutive days of the growing season of 2014 we modelled the daily
20 sap velocities and derived sap flow of these 61 trees and determined the importance of the different predictors.

    Results indicate that a combination of mainly tree-, stand and site-specific factors controls sap velocity patterns in the landscape, namely tree species, tree diameter, the stand density, geology and aspect. For sap flow, the site-specific characteristics geology and aspect were most important. Compared to these predictors, spatial variability of atmospheric demand and soil moisture explains only a small fraction of the variability in the daily datasets. However, the temporal
25 dynamics of the explanatory power of the tree-specific characteristics, especially species, are correlated to the temporal dynamics of potential evaporation. We conclude that transpiration estimates at the landscape scale would benefit from not only considering hydro-meteorological drivers, but also including tree, stand and site characteristics in order to improve the spatial and temporal representation of transpiration for hydrological and soil-vegetation-atmosphere transfer models.

1 Introduction

30 Transpiration makes up to 65 % of total terrestrial evapotranspiration and it is a key process in the hydrological cycle, but knowledge about transpiration fluxes in landscapes is still poor (Jasechko et al, 2013). The main controls of this water flux Iin vegetated ecosystems are, plant-physiological and soil characteristics. are the main controls of this water flux towards the atmosphere. The magnitude and dynamics of transpiration in turn affect the system's energy balance, soil water storage, groundwater recharge and stream flow (Barnard et al., 2010; Bond et al., 2002; Fahle and Dietrich, 2014; Moore et al., 2011;
35 Pielke Sr, 2005). Spatial patterns of transpiration affect hydrological processes and feedbacks within the catchment and are therefore important to consider in distributed hydrological modelling. While most of these models rely on estimates of evapotranspiration gained from meteorological measurements, for example using the Penman-Monteith equation, a better representation of spatio-temporal transpiration dynamics can inform model setups (Fenicia et al. 2016), serve for multi-

response evaluation of models (Loritz et al., 2017; Scudeler et al., 2016) and improve model performance (Seibert et al. 2017). However, studies on the influences on spatial patterns of transpiration in landscapes are still scarce. ~~Hence, understanding and quantifying transpiration and its landscape-scale variability is essential for management decisions and can help to improve the parameterisation of hydrological and soil-vegetation-atmosphere transfer models.~~

Methods to measure transpiration span a wide range of scales, from water and CO_2-exchange measurements on individual leaves to characterising the convective boundary layer which integrates transpiration at the landscape scale. At the plot and stand-level scale, eddy-covariance techniques are applied, whereas at the tree scale, measuring xylem sap velocity and deriving sap flow by including an estimate of the sapwood area is a common method. Determining transpiration of stands using sap flow entails the challenges of reliably estimating whole-tree water use and applying appropriate empirical relationships when upscaling to stands (Köstner et al., 1998). However, for the investigation of main controls for individual trees' water use, sap flow measurements are a suitable tool.

Atmospheric conditions and water availability are the main temporally variable abiotic controls for sap flow, influencing hourly, daily and yearly dynamics (Bovard et al., 2005; Clausnitzer et al., 2011; Ghimire et al., 2014; Granier et al., 2000; Oren et al., 1996; Schume et al., 2004). However, ~~apart from the general boundary conditions, a set of~~ tree-, stand- or site-specific characteristics can also govern~~s~~ the magnitude of sap flow. At similar external conditions, different tree species show contrasts in sap flow due to their ~~respective~~ different hydraulic architecture~~s~~ and ~~coping~~ mechanisms for coping with water stress (Bovard et al., 2005; Gebauer et al., 2012; Oren and Pataki, 2001; Traver et al., 2010). Tree diameter and thus tree size and crown area affects not only ~~absolute~~ sap flow rates, but ~~differences in stem diameter might~~ also ~~entail different~~ radial sap velocity patterns (Bosch et al., 2014; Hölscher et al., 2005; Lüttschwager and Remus, 2007; Vertessy et al., 1995). Within stands, variation in sap velocity can occur because of competition for light and water resources, depending on the species composition (Cienciala et al., 2002; Dalsgaard et al., 2011; Gebauer et al., 2012; Oren and Pataki, 2001; Vincke et al., 2005).

At the landscape scale, site-specific characteristics such as geology, soil type, soil depth or depth to groundwater, elevation, slope position and aspect could potentially control spatial sap flow patterns because of their influence on water and energy availability. Many of these characteristics can be derived from maps and digital elevation models and quantifying their importance is thus especially interesting for modelling purposes requiring landscape-scale transpiration. For instance, the geological setting and associated soil types determine soil water holding capacities, the location of the tree within the landscape's topography can influence its access to groundwater resources and the stand's microclimatic conditions, and differences of aspect also entail variation in energy input (Čermák and Prax, 2001; Vilhar et al., 2005). However, ~~only~~ few studies have focused on the relative strength and possible temporal dynamics of these controls. While the impact of differences in accessible soil volume and groundwater depth on sap flow dynamics has been well described (Angstmann et al., 2013; Čermák and Prax, 2001; Tromp-van Meerveld and McDonnell, 2006), there have been few attempts to empirically use geological or soil units as large-scale proxies for water availability or potentially also for rooting depth limitations (Boer-Euser et al., 2016).

Slope position and elevation have been investigated as site-specific controls of sap flow that~~, which~~ possibly influence soil characteristics and microclimate, ~~have been investigated~~ at a few sites. Bond et al. (2002) report no significant differences in sap flow with slope position for red alders and Douglas fir in Oregon, whereas Kumagai et al. (2007) found larger sap flux density values for cedars in a downslope stand compared to upslope trees~~;~~ however, this effect was confounded by differences in tree size~~s~~ and stand structure, so that transpiration for the stands did not differ between the two slope positions. Similarly, i~~I~~n a drought-prone eucalypt forest in Australia, Mitchell et al. (2012) ~~also~~ attribute lower sap flow values at their upslope plot compared to downslope positions to the differences in stand structure (lower basal area and sapwood area) and lower LAI. Otieno et al. (2014) compared two stands of subtropical evergreen forest in China at two different elevations and highlight the structural differences of the two stands, but ~~also~~ did not find differences in stand

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transpiration. However, differences were found among individual trees and were attributed to tree size as well as social position of the crown. Jung et al. (2014) studied the elevation aspect in deciduous forests on a mountain slope in South Korea at three different elevations, at 450 m, 650 m and 950 a.m.s.l, and found a decrease of total annual canopy transpiration with elevation as a consequence of decreasing length of the growing season, hence of differences in local climate. Maximum Ssap flux density of individual trees during clear-sky days, however, did not vary significantly due to these effects. Using a geostatistical approach, Adelman et al. (2008) studied a suspected influence on transpiration due to differences in water availability on a slope inducing contrasts in species composition, however they did not see this effect in the data, possibly because of overall seasonal dryness during the study period. Another study on controls of patterns of spatial autocorrelation in an extensive sap flow data found the clear species influence on transpiration patterns, however, the effect of a slope-related moisture gradient could not be confirmed (Loranty et al., 2008), adding to the contrasting findings about the influence of slope position on transpiration we see in the literature.

While Even though hillslope aspect at least partially controls radiation input, sap flow studies on the influence of aspect are scarce. In a simulation study, Holst et al. (2010) examined water balances for two beech stands on opposite slopes in Southwest Germany and found higher transpiration values for the south-west slope compared to the north-east slope, which the authors explained with the higher evaporative demand and higher precipitation input on that slope. Focusing on limits of atmospheric exchange, Renner et al. (2016) found that stand composition compensated differences in sensitivities of sap velocity to evaporative demand on the south- and north-facing slopes of a valley transect, which led to overall similar transpiration rates on both slopes.

To summarize, Tthe reported studies have shown that in addition to the obvious atmospheric and tree-scale physiological controls, site-specific characteristics can influence landscape-scale sap flow patterns in a landscape. So far this influence has mainly been studied as individual plot comparisons or on a seasonal basis However, this approach, which does not provide information on the possible short-term, day-to-day changes in the importance of the different controls as a consequence of varying hydro-meteorological conditions. Yet estimating the dynamics of the various controls of sap flow is essential for understanding and predicting spatial patterns of transpiration at the landscape scale.

In this study we aim to exploreWe wanted to know if we can explain daily spatiallandscape-scale patterns of sap velocity and derived sap flowtranspiration at the landscape scale, by applying multiple linear regression models, identifying the influence of based on tree-, stand- and site-specific characteristics that could be gained from maps or surveys and hence would be available for modelling purposesand how the explanatory power of these characteristics is changing over time. We also wanted to exploreexamine the temporal dynamics of these influences and to what extent this can be linkedif site characteristics become more relevant for landscape-scale transpiration patterns under certain conditions and if the combination and strength of dominant controls can be related to hydro-meteorological conditions. Our analysis is based on daily multiple linear regression models for an extensive sap velocity dataset, measured on 61 beech and oak trees on 132 consecutive days in the growing season of 2014, spread over 24 locations in a 290 km²-catchment in Luxemburg.

2 Methods

2.1 Study site

The study site is located in the Attert catchment in western Luxemburg. The catchment covers three geological units (Fig. 1), predominantly Devonian schists of the Ardennes massif in the northwest, Triassic sandy marls, and a small area underlain by Luxemburg sandstone (Jurassic) on the southern catchment border (Martínez-Carreras et al., 2012). These different geological units gave rise to soils with different water retention properties. The soils on schists developed to haplic Cambisols, the soils on marls can be classified as different types of Stagnosols depending on their clay content of 20-60 % and the sandy textures on the Luxembourg sandstone gave rise to Arenosols. The soils were classified according to the WRB

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classification system (IUSS Working Group WRB, 2006) and described further by Sprenger et al. (2016). Plant available water was determined from mean water retention curves (using water tensions at 60hPa and $10^{4.2}$ hPa) based on 120 soil samples (Jackisch, 2015), amounting to 0.30 m³/m³ for Cambisols and Stagnosols and 0.25 m³/m³ for the Arenosols. However, the access to water is not only determined by the soil type. For example the Cambisols in the schist are very

5   shallow and ~~exhibit~~ of high rock content. There are cracks filled with soil material in the underlying schist which could provide water for tree roots. The Stagnosols in the marls area are very clayey in the subsurface, probably limiting plant-available water resources and root penetration in these layers. We observed maximum rooting depths, averaged for each soil type, of 68 cm for the Cambisols, 90 cm for the Stagnosols and 98 cm for the Arenosols (Sprenger et al., 2016). Mean annual precipitation of the study area is approximately 850 mm (Pfister et al., 2000). Land use varies from mainly pasture and

10   agriculture in the marls area, mainly forests in the sandstone to a mixture of agriculture and pasture on the plateaus and forests on the steep slopes of the schist area.

    The catchment is the focus area of the CAOS (Catchments As Organised Systems) research unit which investigates landscape-scale structures, patterns and interactions in hydrological processes for model development (Zehe et al., 2014). A monitoring network of 45 sensor clusters was installed in 2012/2013, covering the different geological units, the land use

15   types deciduous forest and pasture, different slope positions and aspects. Measurements at the individual sites include meteorological parameters such as air temperature and humidity (Campbell CS215) and solar radiation (Apogee Pyranometer SP110) as well as soil moisture (Decagon 5TE) at three depths and three locations at each site. Sap flow is monitored with East30 Sap Flow Sensors at all 29 forest sites.

    The forests covered by the monitoring network mainly consist of mixed deciduous stands with European beech (*Fagus*

20   *sylvatica* L.), pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl., common hornbeam (*Carpinus betulus* L.) and a few maples (*Acer pseudoplatanus* L.) and alders (*Alnus glutinosa* (L.) Gaertn.). However, in this study only the most common species, beech and oaks are considered.

Figure 1: Map of the study site, the Attert catchment in Luxemburg.

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2.2 Sap velocity measurements and calculation of sap flow

The sites in the forest were characterised with a forest inventory on 20 x 20 m² plots, recording stem numbers, diameter at breast height (DBH) and basal area (BA) for all trees with a circumference of more than 4 cm, and tree height for a

30   representative subset of the trees in the stand. Heights~~Tree heights were measured for a representative subset of the trees in the stand; heights~~ were gauged roughly as the canopy tops were not always clearly visible and ~~probably reflect rather~~ we were interested in the social status of the trees rather than the precise height. Four trees per site were selected for sap flow sensor installation. The tree ~~s~~species and diameter were chosen to roughly represent the stand structure at the site but also allow a~~enable~~ comparison to other sites where possible. Sap flow sensors were installed at breast height on the north-facing

35   side of the stem and protected with a reflective cover to minimise the effects of radiation-induced changes in stem temperatures. After removing the bark, holes for the sensors were drilled using a drilling guide to ensure parallel installation of the sensor needles. The sensors, manufactured by East30Sensors in Washington, US, use the heat ratio method with a central heater needle and a thermistor needle upstream and downstream of the heater. Each thermistor needle contains three thermistors, at 5, 18 and 30 mm depth in the wood. Sap velocities (V_{sap} in m s^{-1}) at each of these locations are calculated

40   from the temperatures measured at the corresponding thermistor pairs according to Eq. (1) (equations after Campbell et al., 1991):

$$V_{sap} = \frac{2k}{C_w(r_u+r_d)} \ln\left(\frac{\Delta T_u}{\Delta T_d}\right) \quad (1),$$

where k is the thermal conductivity of the sapwood, set to 0.5 W m^{-1} K^{-1}, C_w is the specific heat capacity of water (J m^{-3} K^{-1}), r is the distance (m) from the heater needle to the thermistor needle (in our case 6 mm) and ΔT is the temperature difference (K) before heating and 60 seconds after the heat pulse. Subscripts u and d stand for location upstream and downstream of the heater.

We corrected these values to account for wounding of the xylem tissue caused by the drilling according to the numerical model solutions for the heat pulse velocity method suggested by Burgess et al. (2001):

$$V_c = bV_{sap} + cV_{sap}^2 + dV_{sap}^3 \quad (2),$$

where V_c is the corrected sap velocity (m s^{-1}) and b, c and d are correction coefficients; for our 2 mm-wounds we use b = 1.8558, c = -0.0018 s m^{-1}, d = 0.0003 s^2 m^{-2} (Burgess et al., 2001). We used ~~Upscaling sap velocities to whole-tree water use is prone to uncertainty because of the azimuthal variation in sap velocities, differences in sap wood depth and sap wood conductivity with depth. We decided to avoid these additional uncertainties and use~~ daytime sap velocity, averaged over a 12-hour window from 8am to 8pm~~, as comparable measurement among trees of different species, admitting that the tree water fluxes will differ from this value mainly due to size and species-specific sap wood characteristics~~. Our sensors provide measurements at three depths (5, 18 and 30 mm) within the sapwood, but ~~. Since radial sap velocity profiles differ between species and tree sizes, and~~ because the sensors were not always ideally installed in the sapwood, we use the maximum value of these three depths' velocities ~~as a reliable measure~~ for the sap velocity part of our analyses.

Calculation of sap flow from sap velocity requires estimates of sapwood area and bark thickness. Sapwood area was calculated using the power law function for sapwood area based on DBH which was originally developed by Vertessy (1995). Coefficients for beech were taken from Gebauer et al. (2008), and for oak from Schmidt (2007), yielding the following equations:

$$A_{S\_B} = 0.778 * DBH_B^{1.917} \quad (3)$$

$$A_{S\_O} = 0.065 * DBH_O^{2.264} \quad (4)$$

with A_S for the sapwood area (cm²), *DBH* is the diameter at breast height (cm), and subscripts are O for oak and B for beech.

The next step was to calculate the sapwood depth. From the whole-tree diameter we first subtracted an estimate for the bark to consider only the sapwood and heartwood part of the stem in the subsequent calculations. Bark thickness was estimated according to empirical relations developed by Rössler (2008):

$$d_{b\_B} = 2.61029 + 0.28522 * DBH_B \quad (5)$$

$$d_{b\_O} = 9.88855 + 0.56734 * DBH_O \quad (6)$$

where d_b is the double bark thickness (mm), *DBH* and subscripts are analogous to Eq. (3) and (4).

Then we calculated the depth of the sapwood-heartwood boundary. As our sensors measure at the three depths 5, 18 and 30 mm, we assigned the corresponding velocities to the stem sections 0-15 mm, 15-25 mm and assumed a linear decline from 25 mm depth the up to the sapwood-heartwood boundary, using the 30 mm velocity as the maximum value of the linear decline (as used by Renner et al., 2016). The linear decline mainly applied to beech trees, as most of the smaller oaks' sap velocities at 30 mm depth were already zero. Daily sap flow for each tree was then derived by multiplying each depth's sap velocity (averaged over the 12 hours from 8am to 8pm as we did before) with the respective sapwood area sections.

We included sap flow in our analyses because, compared to sap velocity, it provides a better estimate of tree transpiration and is usually more of interest for hydrologists. It needs to be noted that the calculation relies on the published species-specific empirical relationships for sapwood area based on tree diameter (eg. Gebauer et al., 2008; Meinzer et al., 2005; Vertessy et al., 1995). Other potential controls on transpiration such as topography or geology as proxies for rooting depth or water availability are not considered in these equations. As site characteristics can induce ecophysiological adaptations, for example in tree functional traits such as stomata density or xylem vessel numbers (González de Andrés et al., 2017; Hajek et

al., 2016; Stojnić et a., 2015), sapwood area properties might be similarly adapted to site conditions. However, to our knowledge there are no studies at the landscape scale yet which examine these adaptations.

Sap velocity is independent of these considerations; therefore, we mainly focus our analyses on this variable and use sap flow as a tentative comparison. For a more reliable way of estimating sap flow influences in a diverse landscape, the sapwood area would need to be measured directly for each tree.

2.3 Auxiliary variables: estimating potential evaporation and water availability

The main environmental limitations to sap flow are the atmospheric conditions (the solar heating of the leaves, water vapour pressure deficit, etc.) as the driving gradient for transpiration and the water supply to the trees. We assess these influences by using a thermodynamically derived measure for potential evaporation E_{pot} which has been recently developed by Kleidon & Renner (2013) as well as the soil moisture observations at each sites as a measure of water availability.

Soil moisture was measured in three profiles per site at 10 cm, 30 cm and 50 cm depth. For our analyses we took the average across all depths and profiles to estimate the average soil moisture in the top 60 cm for each site.

E_{pot} was calculated as follows (Kleidon & Renner, 2013):

$$E_{pot} = \frac{1}{\lambda} \frac{s}{s+\gamma} \frac{R_{sn}}{2} \qquad (7)$$

where $\lambda = 2.5 \cdot 10^6$ Jkg^{-1} is the latent heat of vaporisation, s is an empirical approximation of the slope of the saturation vapour pressure curve, calculated as $s = s(T) = 6.11 \cdot 5417 \cdot T^{-2} \cdot e^{19.83-5417/T}$, with the temperature T (K). The psychrometric constant was approximated as $\gamma \approx 65$ PaK^{-1}, and R_{sn} (W/m²) is absorbed solar radiation. The air temperature was taken from the measurements within the stands at the forest sites. This gives room for some error, as the below-canopy temperature will differ from the above-canopy temperature. However, the temperature does not have very strong leverage in Eq. (7) and we would expect even larger errors if we were to use air temperature from nearby grassland sites because of the differences in microclimate and energy balance for the different land covers. Solar radiation features more prominently in the equation and therefore needs careful estimation. We use an approach deriving the above-canopy radiation from the digital elevation model of the catchment, using the GRASS GIS package r.sun. This method corrects for latitude, day of year and topography and corresponds well with the measured radiation at the pasture sites for cloudless days. Dividing the r.sun-estimated radiation values with the measured radiation values at each pasture site yields correction factors for actual cloud conditions for each day. We apply this cloud correction to the r.sun values for the forests, using the pasture site that is closest to the respective forest sites. These latitude-, topography- and cloud-corrected radiation estimates are then used for calculating E_{pot}. Studying transpiration along a hillslope transect, Renner et al. (2016) found E_{pot} comparable (if slightly underestimating) to a traditional Penman-Monteith approach and also tested for effects of vapour pressure deficit and wind speed. The results did not show distinct effects, hence we used E_{pot} as a robust measure which is appropriate to the available atmospheric measurements in our study.

We also used the radiation measurements within and outside the stands to determine the period when the canopy is fully developed and only use this period for our analyses. For the year 2014 this period lasted from the 11th of May to the 20th of September amounting to 132 days.

2.4 Data analysis

We selected a dataset of continuous sap velocityflow measurements from 61 trees located at 24 of the altogether 29 forest sites in the CAOS dataset. Each of the monitored trees wais associated with tree-, stand- and site-specific properties. Tree-specific properties awere the species, diameter at breast height (DBH) and tree height, whereas the stands are were

characterised by the measurements undertaken in the forest inventory, namely basal area (BA) and median DBH of the stand as well as the number of stems recorded on the inventory plot. Additionally, there ~~a~~were several landscape attributes which c~~an~~ould be associated with the monitored trees such as their position within one of the three geological units, their location on a hillslope and the aspect of that slope. These attributes c~~an~~ould be considered as proxies for associated soil properties

5 and energy availability influencing water availability and potential evaporation. The site characteristics and species enter~~ed~~ the linear models as categorical variables. An overview of the dataset ~~in relation to all tree , stand and site specific characteristics~~ is shown in Table 1, whereby the class "no-slope~~Plain~~" for slope position refer~~s~~ to ~~the~~ slopes ~~with~~of less than 5°~~ slope angle~~, which are located in the marls area. The class "no-aspect~~Flat~~" for aspect includes the same sites, however additionally ~~less steep~~flat downslope parts of four slopes in the schist and sandstone areas. Both classes probably describe

10 landscape positions with shallower depth to groundwater than the other sites.

Table 1: Overview of characteristics associated with the trees in the sap velocity ~~the properties of the sap flow tree~~ dataset. These are used as predictors in the multiple linear regression. Abbreviations are DBH for diameter at breast height, BA for basal area of the stand.

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Potential evaporation and water availability are usually considered as main external dynamic controls of sap flow, so we examined their importance for the temporal variability in sap velocity by correlating the time series of sap velocity with E_{pot} and soil moisture, using the Spearman rank correlation. However, we were interested primarily in the spatial variability of sap velocity as a way to determine influences on transpiration patterns at the landscape scale. We assessed this by

20 examining the spatially distributed dataset of daily-averaged sap velocity of the 61 trees, for each of the 132 days of our study period.

    In a first step, we examined the individual influence of the different tree-, stand- and site-specific controls listed in Table 1 and of the external controls soil moisture and E_{pot} ~~at the respective forest sites,~~ on sap velocity at the respective forest sites, averaged across the study period, separately for each tree. This first analysis ignored ~~the~~ multivariate interaction~~s~~ to get a

25 simplified overview of the data~~,~~; hence effects seen in these comparisons should not be over-interpreted ~~because the controls are considered individually and in reality most likely have a combined effect~~. For the categorical variables (species, geology, slope position and aspect) we also looked at possible temporal changes of differences in sap velocity between the categories by testing daily datasets with the Mann-Whitney-U or the Kruskal-Wallis test, for variables consisting of three or two categories, respectively, to a significance level of α= 0.05.

30   The multidimensional effect of all tree-, stand- and site-specific influences was then analysed with multiple linear regression models separately for each day. This modelling approach is meant to explore the main controls of sap velocity or sap flow patterns, but at this stage we do not aim at predicting these spatial patterns. The response variable for each of the 132 daily models was the log-transformed daily sap velocity of each tree, because the logarithmic values corresponded better to a normal distribution. The linear regression model can be expressed as

35
$$\ln(V_{sap}) = \beta_0 + \sum_{i=1}^{n} \beta_i x_i, \qquad (84)$$

with n predictors ($x_0, ... x_i$), and the regression coefficients ($\beta_0, ... \beta_i$) estimated to obtain an optimum fit.

    Before applying the regression models, we checked the predictors for collinearity by determining the correlation matrix. There was only one combination of predictors with a Spearman rank correlation coefficient above the widely employed critical value of collinearity, $|\rho| > 0.7$ (Dormann et al., 2008; Tannenberger et al., 2010), the number of stems and median

40 diameter of the stand, at $\rho = - 0.73$. The effects of this correlation on the linear models was tested by running the models for both the original set of predictors and again, leaving out number of stems. As the results did not differ with respect to the variance contributions of the different predictors, we kept all predictors in the final analysis. We also did not include

interaction terms in the final models because after testing with various interactions, these did not contribute much to the explained variance.

Although a step-wise simplification of the models using the Akaike information criterion led to a higher percentage of explained variance by the models, we refrained from using this simplification in order to keep the model structures similar for each day to allow comparability of the temporal, day-to-day changes in predictor importance. For prediction, the potentially best model would be more appropriate, however, in our exploratory analysis we focused on comparability. Th~~is~~e relative importance of the predictors for explaining the observed variance of sap velocity~~flow variance or sap flow~~ was assessed using the approach of Grömping (2007), made available in the R package 'relaimpo'. Of the different built-in methods to determine relative importance we used 'lmg'. This method uses sequential sums of squares from the linear model, applies all possible orderings of regressors, and obtains an overall assessment by averaging over all orders, which is deemed appropriate for causal interpretation and unknown weights of the different predictors (Grömping, 2007). The initial order of the predictors in the linear models is not relevant for the relative importance as orderings are shuffled. ~~which is based on a proportional marginal variance decomposition that is more stable and robust than calculating the partial correlation coefficient.~~

Overfitting can be a problem in linear models with many predictors. We checked for this~~To check for overfitting, we~~ by perform~~ing~~ed a comparison between the residual standard error (RSE) of the original models and the root mean square error (RMSE) of a 10-fold cross validation (Fig. 2). In case of overfitting, the RMSE of the cross-validation should be much higher than the RSE. In our case, b~~B~~oth error measures differ~~ed~~ only marginally and ~~a~~were largest when sap velocities we~~a~~re small. These we~~a~~re the days when the linear model generally fail~~s~~ed to explain the variance in the datasets. For days with high sap velocities, the small errors as well as the small difference between RSE and RSME indicated~~show~~ that the models are not overfitted. Additionally, Figure 2 showed~~s~~ that limiting the analysis to the period of fully developed canopy excludes periods of larger errors at the beginning and end of the season.

Figure 2: Comparison of residual standard error of the original linear models (LM-RSE) and the root mean square error of a 10-fold cross validation (CV-RMSE), in relation to mean and standard deviation of daily sap velocities (Vsap). The dashed lines depict the analysis period with a fully developed canopy which we determined from radiation analyses as described in section 2.3.

The linear models for sap velocity give an indication about possible controls of transpiration; however, a more intuitive measure for transpiration is sap flow. Therefore, as an indication of how the actual transpiration patterns are influenced by site- and stand-specific characteristics, we repeated the multiple linear regression analysis with derived sap flow dataset. The calculation from sap velocity to sap flow is based on the species-specific relations between sapwood and DBH, so we did not use Species, DBH and Height as predictors in the linear models for sap flow as they are not independent anymore. We only used the remaining stand- and site-specific predictors as well as E_{pot} and soil moisture.

We analysed the temporal dynamics of the variance contributions of the individual predictors and of the proportion of variance explained by all the tree-specific predictors (only for sap velocity) taken together, all the stand-specific predictors taken together, and all the site-specific predictors taken together ~~the category sums for tree-, stand- and site-specific characteristics~~. We also correlated these time series to catchment-averaged time series of soil moisture and E_{pot} as indicators ~~for~~of general atmospheric demand and water availability, using the Spearman rank correlation. All statistical analyses were carried out in the language and environment R (R Development Core Team, 2014).

3 Results

3.1 Controls of temporal dynamics of sap velocity

Correlations of time series of sap velocity for each tree with E_{pot} and soil moisture yielded high positive and significant (α=
0.05) Spearman rank correlations for E_{pot}, but correlations to soil moisture were slightly negative and very weak (Fig. 3).

5

Figure 3: Histograms of temporal correlations between (a) E_{pot} and (b) soil moisture at each site with sap velocity for the 61 trees in the dataset. The small numbers in grey on top of the bars indicate how many of the correlations in the specific group are significant.

10 **3.2 Controls of spatial patterns in daily mean~~spatial patterns of~~ sap velocity and sap flow**

A first simplified overview of the influence of the various factors on sap velocity patterns was derived from plotting sap
velocity, averaged over the entire study period for each tree, against the factors or their respective categories (Fig. 4).
Obviously, this graph neglects the combined influence of the interplay of all these factors, but yields a first overview of the
data and possible relations. For example, the difference between higher sap velocities in beech trees compared to oaks can be
15 seen as well as a possible positive relation between sap velocity and DBH or tree height. In the category Aspect, the boxplots
show a difference between higher sap velocities on north-facing slopes compared to south-facing ones, with trees located in
plains having somewhat intermediate velocities.

20 **Figure 4: Univariate influence of each predictor on sap velocity means for each tree over the entire study period. Boxplot parameters are as follows: the horizontal line within the box visualises the median, boxes comprise data between the 1st and 3rd quartile of the data, whiskers reach to 1.5 × the interquartile range outside the box (or to the maximum/minimum value if smaller/larger), circles stand for outliers/data points outside the whiskers, notches show approximately 95% confidence intervals around the medians.**

~~**Figure 4: Individual influence of each factor on sap velocity means for each tree over the entire study period.**~~

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The categorical factors were assessed in more detail looking at temporal changes in sap velocity differences. Statistical tests
(Mann-Whitney-U for two and Kruskal-Wallis for three categories, α= 0.05) applied to the sap velocity datasets for each day
for the example of the categorical factors geology, species, slope position and aspect showed significant differences (Fig..5).
There is in particular a significant difference between south- and north-facing slopes and between beech and oak trees for
30 most days of the dataset (Fig. 5), providing a first indication of the importance of both tree- and site-specific influences. In
contrast, there were only 36 of 132 days showing significant differences for geology and 25 days for slope position,
occurring when sap velocities were generally low.~~few days with differences in geology or slope positions.~~

35 **Figure 5: Differences between sap velocities depending on (a) geology, (b) species, (c) slope position and (d) aspect. Lines show average dynamics of each class. Asterisks at the bottom of the panels indicate significant differences for that day according to Mann-Whitney-U or Kruskal-Wallis tests at α= 0.05, for differences between the two or three categories, respectively.**

~~**Figure 5: Influence of (a) geology, (b) species, (c) slope position and (d) aspect on daily sap velocity patterns. Lines show average dynamics of each category. Asterisks at the bottom of the panels indicate significant differences for each day according to Mann-Whitney-U or Kruskal-Wallis tests at α= 0.05, for differences between the two or three categories, respectively.**~~

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In a more comprehensive approach, we assessed the combined effect of the various tree-, stand- and site-specific influences
on sap velocity with the help of multiple linear regression generating 132 daily models describing the spatial patterns. The
total explained variance for the sap velocity models ranged from 20%, on days when the models fail to explain the spatial

variability in the dataset, to 72%, which constitutes fairly good explanatory power (Fig. 6). The total explained variance correlated strongly with catchment averages of sap velocity (Pearson's r = 0.84, p < 0.001), especially at sap velocities > 7 cm h⁻¹ (Fig. 7). Spatial variability of sap velocity in the catchment, expressed as standard deviation of the daily values for the 61 trees, also increased with increasing mean sap velocity (Pearson's r = 0.98, p < 0.001; Fig. 7). The consistent model structure showed that the change in the proportion of explained variance over time was different for the various predictors (Fig. 6). Averaged across the 132 daily models, 9% of the variance was explained by species~~Mean values for the tree-specific predictors across the 132 daily models were 9% of the explained variance for species~~, 9% ~~for~~by DBH ~~and~~, 4% ~~for~~by tree height. Characteristics of the stand yielded 1% for BA, 1% for median DBH, 4% for number of stems, and the site-specific predictors amounted to 2% for slope position, 4% for geology and 6% for aspect. The external dynamic controls of sap flow, E_{pot} and soil moisture, explained 7% and 3% of the variance in daily sap velocity patterns, respectively.

The contribution of the different predictors to the overall explained variance of the linear models varied strongly from day to day. On days when average and spatial variability of sap velocity was low the models performed badly. There were some predictors which showed larger fluctuations, for example species, compared to more constant contributions from predictors like the number of stems or DBH (Fig. 6).

Figure 6: Proportion of variance explained by the different predictors in the daily linear models of spatial sap velocity patterns: 132 daily models from 61 trees at 24 sites.

~~**Figure 6: Explained variance of daily linear models of spatial sap velocity patterns: 132 daily models from 61 trees at 24 sites.**~~

Figure 7: (a) Explained variance of the linear models in relation to mean sap velocities for all 132 days of the study period and (b) standard deviation of sap velocity depending on mean sap velocities for those 132 days.

The multiple linear regression models for sap flow patterns explained between 18 and 56 % of the variance in the daily datasets (Fig. 8), on average 49 %. Averaged across the 132 daily models, the stand-specific predictors explained 8 % of the variance (4% by BA, 1% by median DBH and 3 % by the number of stems), the largest contribution came from geology with 21%, then aspect with 10%, while slope position only explained 3%. E_{pot} and soil moisture explained 7 % and 1 % of the variance, respectively, which is comparable to their contributions in the linear models for sap velocity patterns.

Figure 8: Proportion of variance explained by the different predictors in the daily linear models of spatial sap flow patterns: 132 daily models from 61 trees at 24 sites.

The variance contributions stayed fairly constant in time, except for days when the models failed to explain the spatial variability in the data altogether (Fig. 8). Compared to the linear models for sap velocity, the models for sap flow had less explanatory power. The contributions of the stand-specific predictors were not very important, similar to the results for sap velocity. For the site-specific controls, the largest contribution came from geology, less from aspect; in contrast, in the sap velocity models, aspect explained a larger proportion of the variance than geology (Fig. 8).

3.3 Temporal dynamics of predictor importance ~~for daily spatial sap velocity patterns~~

Comparing the dynamics of the proportion of variance explained by all the tree-specific predictors taken together, all the stand-specific predictors taken together, and all the site-specific predictors taken together ~~cumulated variance contributions~~

for the groups of tree , stand and site specific predictors to the catchment-average dynamics of E_{pot} and soil moisture (Fig. 98) showsed that the stand- and site-specific predictors' contributions stayed relatively constant apart from the days when the model failed,. This was the case for both the sap velocity and the sap flow models. whereasIn contrast, the tree-specific predictors in the sap velocity models varied to a greater extent. Already visual comparison hints at Visual comparison indicated a link between fluctuations of tree-specific influences and potential evaporation (E_{pot}), but not soil moisture (Fig. 9).

Figure 9: Explained variance of the daily linear models, separated according to the predictor groups used in the regression, (a) for sap velocity and (b) for sap flow. (c) Catchment average of soil moisture and potential evaporation E_{pot}.

Figure 8: (a) Explained variance of the daily linear models, separated according to tree , stand- and site-specific predictors. (b) Catchment average of soil moisture and potential evaporation E_{pot}.

The Spearman rank correlations of the predictors' explained variance with E_{pot} and soil moisture, listed in Table 2, also confirmed that changes in species influence in the sap velocity were strongly linked to changes in E_{pot}, with a significant correlation (at α= 0.05) of r = 0.81. Further weaker but significant correlations were detected between E_{pot} and number of stems at r = 0.50, aspect at r = 0.67 and soil moisture at r = 0.55, respectively. Summarised into categories, the influence of tree-specific predictors strongly correlated with E_{pot} (r = 0.86); similarly, there was a strong correlation of the overall explained variance with E_{pot} (r = 0.84). Some of the correlations with soil moisture were significant, however,but they were mostly weak, with at |r| <= 0.37.

In the sap flow models, the only significant correlations worth mentioning were between E_{pot} and aspect and between E_{pot} and the overall explained variance, at r = 0.57 and r = 0.72, respectively.

Table 2: Spearman rank correlation between the time series of the different predictors' explained variance and the time series of potential evaporation (E_{pot}) and soil moisture. Values in bold italics are significant correlations (at α= 0.05).

4 Discussion

4.1 Controls of temporal dynamics of sap velocity

The strong positive temporal correlation of sap velocity and E_{pot} (Fig. 3) confirms the well-known role of the atmospheric controls E_{pot} as a main external drivers for transpiration (Bovard et al., 2005; Clausnitzer et al., 2011; Granier et al., 2000; Jonard et al., 2011). Soil moisture on the other hand did not affect the temporal dynamics of sap velocity in a similar way (Fig. 3). One reason for this weak relation could be that water is not a limiting factor for transpiration in this landscape, or at least not during the observed time period. For example, in the schist area of the catchment, anecdotal evidence given by forest wardens suggests that beech trees on south-facing slopes are indeed water-stressed during dry, hot summer months, although in our data we did not see a limitation of sap velocity for the beech trees. A different explanation for the lack of correlation is that soil moisture in the top 60 cm of the soil profile is simply not a sufficiently good proxy for water availability. In the soils of the schist there might be additional water resources stored in the weathered bedrock or the schist fractures which could be accessible to roots reaching deeper than the maximum rooting depths estimated from power drill cores in the study area (Sprenger et al., 2016), as these can exceed the average maximum rooting depth in the soil (only 68 cm, estimated from power drill cores; Sprenger et al., 2016). In the deep sandstone soils with average maximum observed rooting depths of 98 cm in the drill cores (Sprenger et al., 2016) roots could also reach deeper, exploiting larger soil volumes or possibly tapping groundwater. The mostly flat marl areas exhibit shallow groundwater tables, so water limitation is unlikely for longer periods during the year. Thus, although water availability is an important boundary condition for

transpiration, soil moisture measurements for the top 60 cm might not be an appropriate proxy, and including available information on groundwater levels or also soil moisture in deeper layers could be useful in that regard. ~~However, successful explanation of temporal transpiration dynamics at individual points is only one necessary aspect for estimating and modelling transpiration. If the goal is to represent hydrological processes at the landscape scale, the spatial representation of transpiration and the identification of the main controls of spatial transpiration patterns are similarly important.~~

4.2 Controls on ~~daily~~ spatial patterns in daily mean sap velocity and sap flow

Even from the simplified univariate assessment, the influence~~relation~~ of characteristics such as species, DBH and aspect ~~to~~on spatial sap velocity patterns is visible (Fig. 4). In the more comprehensive approach applying multiple linear regression models to the daily sap velocity datasets, the combined effect of tree-, stand- and site-specific predictors surpasses by far the explanatory power of the boundary conditions, as E_{pot} and soil moisture (Fig. 6) together explained only around 10% of the variance in sap flow patterns (Fig. 6). From the larger spatial variability of soil moisture (average of spatial standard deviation of 5 Vol.%, compared to an average of temporal standard deviation of 2 Vol.%) some influence on spatial sap velocity patterns might have been expected. But similar to the lack of temporal correlation with soil moisture, the lack of importance for spatial variability could result from the fact that measurements in the top 50 cm of the soil column were not meaningful to assess water availability at the sites or that a soil moisture limitation was not occurring in the observation period. E_{pot} held larger explanatory power, but compared to the importance for temporal variability in sap velocity, the spatial effect was very small, possibly because the range of spatial variability in E_{pot} is much smaller. (The average of spatial standard deviation of E_{pot} was 0.18 W m^{-2}, whereas the average of its temporal standard deviation was 0.73 W m^{-2}). The same argument holds true for the similarly low proportion of explained variance by E_{pot} in the linear models for sap flow. This suggests that spatial patterns of (evapo)transpiration for distributed hydrological models based on meteorologically-derived estimates only reflect a small part of the spatial variability of measured transpiration.

The explained variance of the tree-specific characteristics amounted to 22 % averaged over the 132 sap velocity models (Fig. 6). Mechanisms underlying the differences in sap flow related to species, tree diameter and height have been studied in great detail in the field of tree physiology. The species contrast in our case consists of higher sap velocities for beech, as beech shows physiological advantages in transpiration efficiency and outperforms ~~the~~ oaks in sufficiently moist conditions (Hölscher et al., 2005). Sap flow contrasts are even more pronounced because the active sapwood of oaks is limited to the outermost few annuli whereas for larger beech trees it can easily reach a depth of 7 cm or more (Gebauer et al., 2008). This limitation for oaks is visible in the species-specific allometric equations for sapwood area (Eq. 3 and Eq. 4), but additionally, sap velocity in the innermost of our sensors (at 30 mm into the tree) was frequently zero for oaks. As expected, forest species composition is a major determinant of transpiration patterns (eg. Hernandez-Santana et al., 2015, Loranty et al, 2008).

Tree height and DBH contrasts probably reflect the differences in social status, with larger, dominant trees reaching higher transpiration values than understorey trees. That larger trees, both ~~higher~~ taller and with larger DBH, exhibit higher sap velocities is likely due to their associated larger canopy and root volume, ensuring on the one hand the exposure of the leaves to the atmospheric gradient, on the other hand having access to a larger soil volume and potential water supply (Bolte et al., 2004; Nadezhdina and Čermák, 2003). For sap flow, the contrasts are again even larger than for sap velocity, because not only is larger DBH associated with larger velocities, but according to Eq. 3 and Eq. 4, larger DBH also entails larger sapwood area, multiplying the effect of the sap velocity differences. Implementing spatial patterns of tree sizes into hydrological models could be attempted using mapped information from forest inventories, management plans or even LiDAR images (Ibanez et al., 2016; Rabadán et al., 2016; Vauhkonen et al., 2015).

The stand density, expressed ~~as~~by the number of stems, explained on average 4% of the variance in the daily models for sap velocity and 3% for sap flow. Decreasing sap velocities with increasing stand density hints at the competition for light and resources among individual trees (Cienciala et al., 2002; Dalsgaard et al., 2011; Gebauer et al., 2012; Oren and Pataki,

2001; Vincke et al., 2005). However, due to this small contribution the linear models, the stand-specific influence should not be over-interpreted. Basal area contributed on average 4% to sap flow models and hints at the same mechanisms as stand density.

~~However, in our study, t~~The site-specific predictors together explained on average 12% of the spatial variance in the sap velocity models and 34% in the sap flow models (Fig. 6 and 8). ~~we included because they might be deduced from readily available distributed datasets, were more important than stand characteristics to explain daily sap velocity patterns. The average combined explained variance of these predictors of 12% showed that considering these predictors can help to improve estimates of landscape-scale transpiration variability.~~

Landscape characteristics such as topography and geology will control sap velocity patterns of otherwise homogeneous forests because they influence spatial patterns of either water or energy availability. Topography ~~is~~ primarily control~~sling~~ radiation input, and to some extent water availability through depth to groundwater and ~~also~~ soil characteristics, while geology ~~is~~ mainly control~~sling~~ root distribution and water availability because it determines the depth to bedrock, ~~and~~ depth to groundwater as well as soil type and soil depth. The effect of soil depth on transpiration, for example, has been shown by Tromp-van Meerveld and McDonnell (2006) for soils of the same ~~soil~~ type on the Panola hillslope, and the contrasts between different geological units in the Attert basin are likely to be even more pronounced. The soils in the schist area are very shallow, restricting rooting depth to an average of 68 cm (Sprenger et al., 2016). ~~and t~~Together with moderate values for plant-available water (Jackisch, 2015), which are probably even ~~lessened~~ lowered by the high rock content, this could ~~possibly~~ lead~~ing~~ to the smaller sap velocities in the schist compared to the sandstone or marls. These differences in soil depth and water retention characteristics ~~on different geological units affect landscape-scale~~ manifest in differences in hydrological ~~processes~~ characteristics such as water storage dynamics, leading to~~which can be seen in the differences in~~ contrasting runoff generation mechanisms for ~~between~~ schist, marls and sandstone areas in the Attert catchment (van den Bos et al., 2006; Wrede et al., 2015). In turn, these geology-induced contrasts in d~~D~~epth to groundwater and ~~the geological setting of the water~~ storage control tree access to these ~~storage systems~~water reservoirs and favour species with adapted rooting systems (Dalsgaard et al., 2011), thus introducing a landscape-scale effect on sap flow. We see this effect in the sap velocity models and even larger in those for sap flow, suggesting that including geological maps into distributed hydrological models could be helpful not only for soil and bedrock characteristics but also for transpiration patterns.

The influence~~variation in~~ of aspect (Fig. 6 and 8) was mainly due to the south-facing slopes having smaller sap velocities and sap flow values compared to north-facing slopes. Possibly, energy input - which would be larger on south-facing slopes - is not the critical factor for transpiration in this landscape. On the contrary, larger ~~As~~ energy input ~~is larger~~ on south-facing slopes~~,~~ might ~~these~~ make them ~~slopes might be~~ more prone to water limitation (Holst et al., 2010), especially when combined with other limiting factors such as the shallow soils in the schist area (which holds a large proportion of the south-facing slopes in our dataset). However, as we did not see acute signs of water limitation in our data, the contrast in sap velocities due to aspect would have to be long-term physiological adaptations to the drier conditions on south-facing slopes. The dominance of geology compared to aspect in the sap flow models could possibly also result from a physiological effect of aspect influencing sapwood area or wood properties which would then already be considered in the sap flow values, leaving geology as an independent predictor more important for spatial patterns in sap flow.

There is an apparent discrepancy between the influence of aspect, with stems from higher sap velocity (similarly for sap flow) values on north-facing slopes and the influence of E_{pot} which manifests in slightly increasing sap velocities for increasing E_{pot} values. We would expect the larger E_{pot} and sap velocity values to be on the south-facing slopes due to the higher radiation input. However, it needs to be noted that the values for E_{pot} are calculated at the respective tree sites and these are not necessarily at the same relative positions on the slopes. So the E_{pot} values are probably not directly related to aspect, but also to the location within the valley, shading effects, etc. Grouping the E_{pot} values according to aspect (data not shown), the main contrast occurs between north-facing slopes having higher values compared to no-aspect, whereas north-

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and south-facing slopes do not show considerable differences. Furthermore, as already mentioned before, spatial variability in the E_{pot} dataset are generally not very pronounced. Thus, a situation where the study trees are situated at more extreme locations with respect to aspect will probably induce a larger effect of E_{pot}.

~~Additionally there might be a sampling effect because the south-facing slopes in our dataset support more oak dominated forests which have generally lower sap velocities compared to beech trees.~~ Slope position did not play a major role in explaining spatial sap velocity patterns (Fig. 6 and 8) although due to its possible effect on soil depth, water availability and species composition it is also the best-studied of the three site properties we included in our models (Adelman et al., 2008; Bond et al., 2002; Kumagai et al., 2007; Loranty et al., 2008; Mitchell et al., 2012). A reason for this lack of explanatory power could be that the information within this variable is partly also included in aspect because both the aspect category "no-aspect~~flat~~" and the slope position categories "no-slope~~plain~~" and "downslope" suggest sites which are close to groundwater resources~~.~~.

In a way, all three ~~the~~ site-specific influences ~~of~~ geology, aspect and slope position can be regarded as proxies for underlying characteristics of water availability. ~~and thus affect landscape-scale transpiration patterns.~~

4.3 Temporal dynamics of predictor importance ~~for explaining the daily spatial sap velocity patterns~~

Understanding the feedback of ~~these~~spatial transpiration patterns with hydrological processes requires assessing the temporal dynamics of ~~site- and tree-specific~~the controls ~~of these patterns on transpiration at characteristic time scales~~, for example on a seasonal or daily basis. Our analyses indicate that ~~landscape-scale~~spatial sap velocity patterns are governed by mainly tree-~~, stand-~~ and site-specific characteristics, for sap flow mainly site-specific, but temporal shifts in these controls depend on hydro-meteorological conditions, especially potential evaporation (Fig. 9). And whereas the direct influence of ~~variability in~~ hydro-meteorological variability~~conditions~~ on sap flow has been highlighted in many studies (Bovard et al., 2005; Clausnitzer et al., 2011; Granier et al., 2000; Jonard et al., 2011), the link between these conditions and spatial patterns of sap flow and their controls is still not well understood. Additionally, most studies which include site-specific controls focus on a seasonal basis or undertake plot comparisons.

The temporal dynamics of the different predictor categories showed contrasting dependency on potential evaporation (Fig. 9). While the stand- and site-specific predictors as well as DBH and tree height remained fairly constant in their total explained variance, for both sap velocity and sap flow, the species~~-, dependent temporal~~explained variance in the sap velocity models was strongly correlated to the dynamics of E_{pot} (Table 2). The species effect in this context is the contrast between oaks, which can only respond to increasing E_{pot} only up to a certain threshold (Fig. 5) and beech trees, which ~~when not water limited,~~ can reach higher sap velocities when they are not water-limited.

A second predictor with considerable positive correlation with E_{pot} is aspect (Table 2). As the south-facing slopes seem to be water-limited for some amount of time and we suspect a physiological adaptation of the trees to this limitation, the differences in sap velocities between north- and south-facing slopes will increase with increasing E_{pot}.

If there was a water limitation on the south-facing slopes, many of the adapted beech trees on these slopes might not be able to use the full transpiration potential that is available to trees on north-facing slopes, and the spatial patterns could shift towards a declined species contrast and lesser temporal variability of this influence as long as the drought persists. At the same time and intermingling, this could lead to a temporally more dynamic influence of aspect. Further studies in a very dry year would help to investigate these interrelations

Lastly, the overall explained variance of our linear models for both sap velocity and sap flow also correlates with E_{pot}·, as it does with sap velocity (Fig. 7). ~~Obviously~~The models can explain considerable proportions of the spatial variability in sap velocity and sap flow when those values themselves can become large, driven by high E_{pot} and thus leading to larger

transpiration contrasts in the landscape, due to for example species or aspect. . ~~the predictors we consider in our study are useful to describe large differences in sap velocity patterns, when high potential evaporation entails contrasts in for example species or aspect.~~ At lower values of potential evaporation, the spatial variability of sap velocity is less pronounced and not primarily determined by the predictors included in our models.

For hydrological modellers this means that at low values of potential evaporation, which likely coincide with cloudy, rainy or cold days, transpiration flux is low and contains little spatial structure. On the one hand this entails smaller potential errors in the transpiration estimates, but on the other hand, it could be considered in attempts to apply dynamic model structures. During low-E_{pot} days, transpiration could be implemented in a more general and aggregated way, whereas during high-E_{pot} days including the spatial patterns of tree, (stand) and site characteristics could markedly improve model performance and spatial representation of transpiration.

~~Finally, it is important to note that we are focusing on sap velocities in this study because of precautions in sensor installation in 2014, leading to non-ideal sensor depths preventing the reliable calculation of sap flow volumes. Additionally, scaling up from sap velocities to tree and stand transpiration entails uncertainties in the representativeness of sap velocity estimation due to circumferential variability, wounding effects and the challenge of determining sap velocity depth profiles and sapwood area. For some of the abovementioned predictor effects the contrasts will be even more pronounced when considering actual sap flow instead of sap velocities. For example, the species effect shows higher velocities for beech compared to oaks. As the active sapwood of oaks is limited to the outermost annuli whereas for larger beeches it can easily reach a depth of 7 cm (Gebauer et al., 2008), the difference in actual transported water and hence transpiration would be even more pronounced. On the other hand, the aspect effect might be not as strong as seen in the sap velocities. Renner et al. (2016) showed in a recent study considering only a few of the sites that differences in sap velocity due to aspect might be countered by variation in the relative sap-wood area for the respective stands. The effects we see in our sap velocity analyses should be studied further and compared to patterns in up-scaled stand transpiration estimates to comprehensively understand the dynamics of landscape-scale patterns of transpiration and their effect on hydrological processes.~~

5 Conclusions

Sap flow measurements are a suitable tool to investigate the different influences that shape spatial patterns of tree transpiration in a landscape. However, there are some uncertainties involved, for example the widely applied calculation of sap flow from sap velocities includes the assumption that the tree species and size are mainly determining this relationship. As ecophysiological adaptations to site conditions have been shown in other contexts, an independent determination of sap flow for each tree in the study would need direct measurements of sapwood area and other relevant xylem characteristics. This would enable a better quantification of the different influences on spatial transpiration patterns which would complement the more exploratory character of our study.

We examined both the influences on spatial patterns of transpiration in a landscape and their temporal dynamics, , by means of sap velocity and sap flow. The spatial patterns were mainly controlled by ~~A combination of~~ tree-~~, stand~~ and site-specific characteristics ~~influenced the observed daily spatial sap velocity patterns~~. The ~~t~~Temporal dynamics of the overall explained variance of the linear models and the relative importance of ~~especially the tree-specific controls were~~species was closely linked to the dynamics of potential evaporation, whereas the site-specific influences remained constant over time. This means that the abiotic characteristics of the landscape control transpiration pattern to a certain extent and this control remains static in time. On the other hand, the importance of biotic characteristics, i.e. the landscape-scale patterns of tree species distribution, varies in time and becomes most important during days of high atmospheric demand.

Our results suggest that spatial representation of landscape-scale transpiration in distributed hydrological models could be improved ~~landscape scale transpiration estimates for management or modelling purposes could benefit from~~ by including

spatial patterns of tree-, stand- and site-specific characteristics. For spatial sap flow patterns, these influences were considerably larger than~~not only~~ the obvious and widely-used influences of the potential evaporation and water availability in the soil. Consequently,~~but also the spatial patterns of sap flow resulting from the interplay of tree-, stand- and site-specific controls at the landscape scale.~~ ~~S~~ similar to resolving agricultural areas according to crops at the field scale, one could

5 represent the spatial structure in forest transpiration resulting from species and size distributions, but also from patterns ~~in water and energy availability~~ due to site characteristics such as geology or topography.~~, in forests that appear homogenous in terms of species and stand structure.~~ This information can be used for model parameterisation or as a part of multiresponse evaluation for soil-vegetation-atmosphere transfer and hydrological models.

Additionally, identifying phases of varying importance of the different ~~predictors~~influences, and their dependence on

10 E_{pot}, can~~ould~~ help modellers decide when to best include site-specific characteristics to describe spatial patterns of transpiration in models, ~~and~~ when a classification according to species and stands might be more appropriate or when it is not necessary at all to implement a spatially explicit transpiration estimate. Thus,~~.~~ the spatial representation of transpiration in hydrological models could be attempted in a temporally dynamic way, and, when spatial structure is needed, be based on information from geological maps, digital elevation models, forest inventories or remote sensing images.

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~~The way forward from these findings should be to address the well known challenge of analysing whole tree water use instead of sap velocities and to attempt the upscaling from trees to stands to obtain a dataset of actual stand transpiration with optimised sensor installation. This data could then be used as a reference for soil vegetation atmosphere transfer and hydrological models. Furthermore, including information from forest inventories and digital elevation models in the multiple~~

20 ~~regression of sap flow datasets and identifying the dominant controls and temporal dynamics could consequently enable the regionalisation and prediction of transpiration processes at the landscape scale using these readily available distributed datasets.~~

6 Acknowledgements

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Table 1: Overview of the ~~properties~~ <u>characteristics associated with the trees in the</u> of the sap ~~flow tree~~<u>velocity</u> **dataset.** <u>**These are**</u>
<u>**used as predictors in the multiple linear regression.**</u> **Abbreviations are DBH for diameter at breast height, BA for basal area of the**
stand.

Property	Group	Class (and # of trees in each class)	Value (25/50/75 percentile)
Species	Tree-specific	~~b~~Beech (39), ~~O~~oak (22)	
DBH (cm)	Tree-specific		34/ 46/ 63
Height (m)	Tree-specific		24/29/ 34
BA (m² ha^{-1})	Stand-specific		27/40/54
Median DBH (cm)	Stand-specific		5/14/28
# of stems	Stand-specific		20/24/43
Geology	Site-specific	~~m~~Marls (13), ~~s~~Sandstone (22), ~~S~~schist (26)	
Slope position	Site-specific	~~U~~upslope (41), ~~d~~Downslope (9), <u>no-slope</u>~~Plain~~ (11)	
Aspect	Site-specific	~~n~~North (17), ~~S~~south(29), <u>no-aspect</u>~~Flat~~ (15)	

Table 2: Spearman rank correlation between the time series of the different predictors' explained variance and the time series of
potential evaporation (E_{pot}) and soil moisture. Values in bold italics are significant correlations (at α= 0.05).

	Sap velocity		Sap flow	
Predictor	E_{pot}	Soil moisture	E_{pot}	Soil moisture
Species	*0.81*	*-0.30*		
DBH	*0.32*	-0.14		
Height	0.11	-0.05		
BA	-0.15	-0.05	*0.44*	*-0.09*
Median DBH	*0.44*	-0.16	*0.34*	*0.00*

# of stems	*0.50*	*-0.35*	*0.44*	*-0.03*
Slope	*-0.32*	*0.21*	*0.22*	*-0.01*
Geology	0.04	*0.18*	*0.35*	-0.20
Aspect	*0.67*	*-0.37*	*0.57*	-0.38
E_{pot}	*0.34*	*-0.18*	0.10	*0.04*
Soil moisture	*0.55*	*-0.30*	*0.25*	-0.21
Tree-specific	*0.86*	*-0.34*		
Stand-specific	*0.28*	*-0.33*	*0.42*	*-0.07*
Site-specific	*0.35*	-0.14	*0.46*	-0.26
Total exp. var.	*0.84*	*-0.38*	*0.72*	-0.37
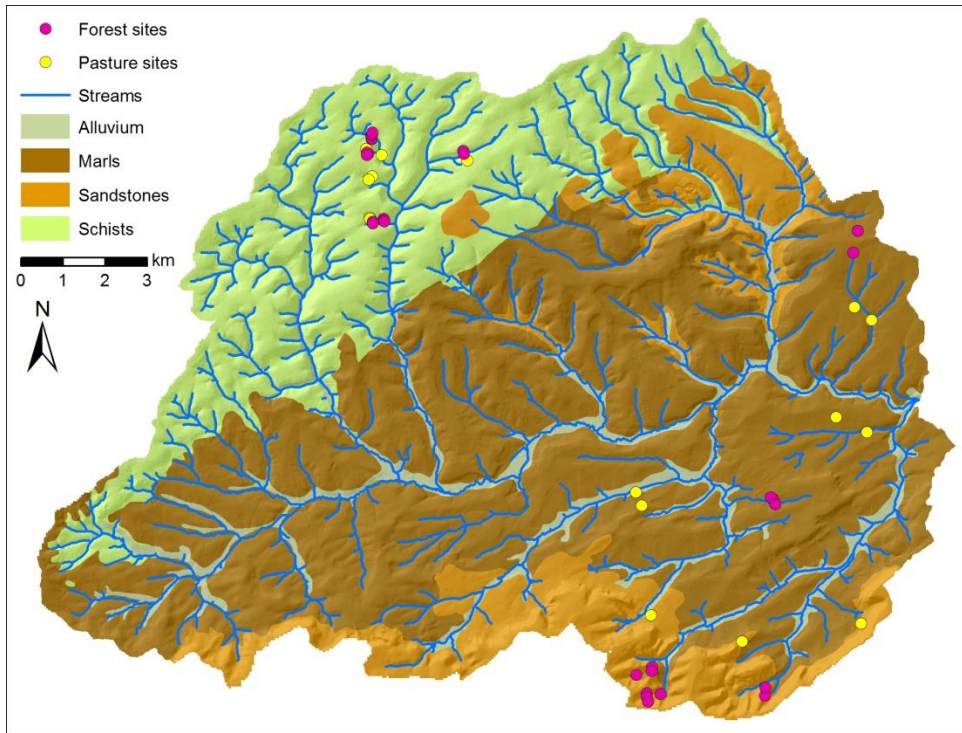
Figure 1: Map of the study site, the Attert catchment in Luxembourg.

5
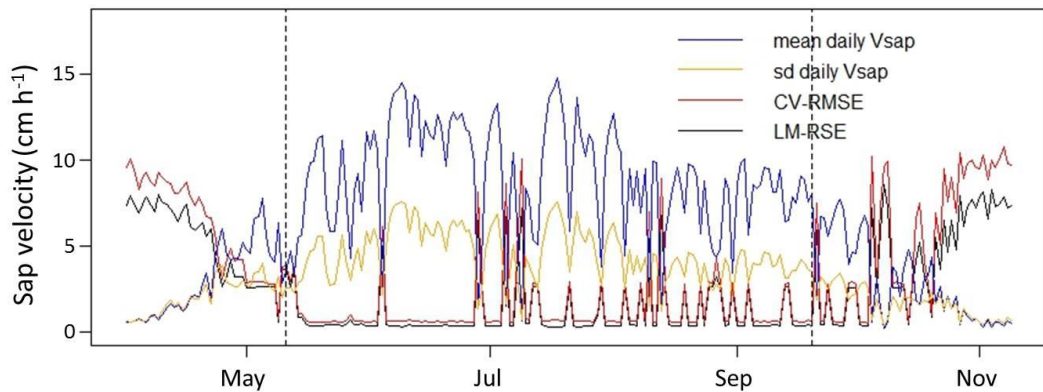
Figure 2: Comparison of residual standard error of the original linear models (LM-RSE) and the root mean square error of a 10-fold cross validation (CV-RMSE), in relation to mean and standard deviation of daily sap velocities (Vsap). The dashed lines indicate the beginning and end of the focus period with a fully developed canopy.
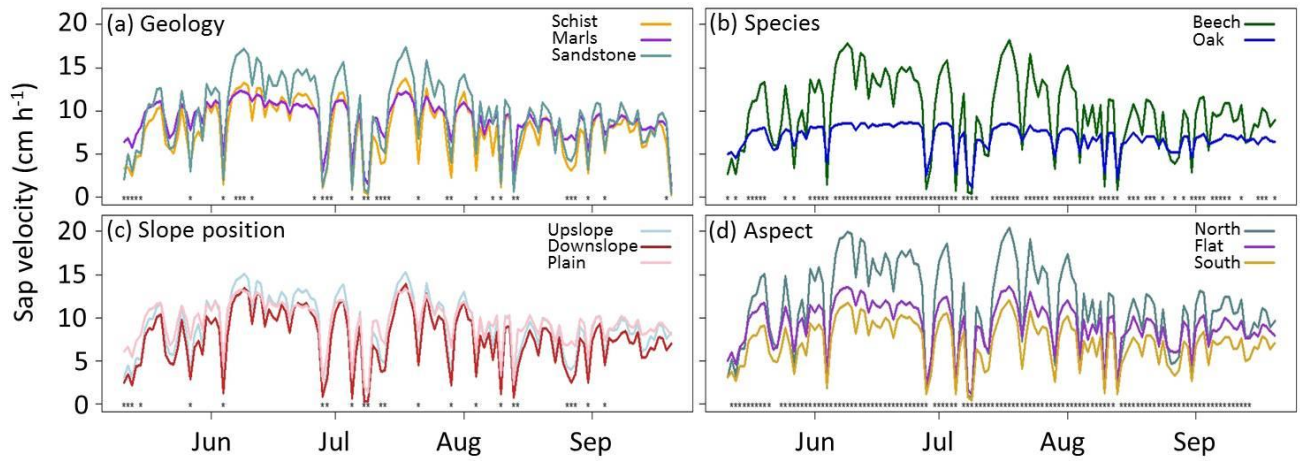
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Figure 3: Histograms of temporal correlations between (a) E_{pot} and (b) soil moisture at each site with sap velocity for the 61 trees in the dataset. The small numbers in grey on top of the bars indicate how many of the correlations in the specific group are significant.

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Figure 4: ~~Individual~~Univariate influence of each ~~factor~~predictor on sap velocity means for each tree over the entire study period. Boxplot parameters are as follows: the horizontal line within the box visualises the median, boxes comprise data between the 1st and 3rd quartile of the data, whiskers reach to 1.5 × the interquartile range outside the box (or to the maximum/minimum value if smaller/larger), circles stand for outliers/data points outside the whiskers, notches show approximately 95% confidence intervals around the medians.

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Figure 5: ~~Influence of~~<u>Differences between sap velocities depending on</u> (a) geology, (b) species, (c) slope position and (d) aspect ~~on daily sap velocity patterns~~. **Lines show average dynamics of each ~~category~~<u>class</u>. Asterisks at the bottom of the panels indicate significant differences for ~~each~~ <u>that</u> day according to Mann-Whitney-U or Kruskal-Wallis tests at α= 0.05, for differences between the two or three categories, respectively.**
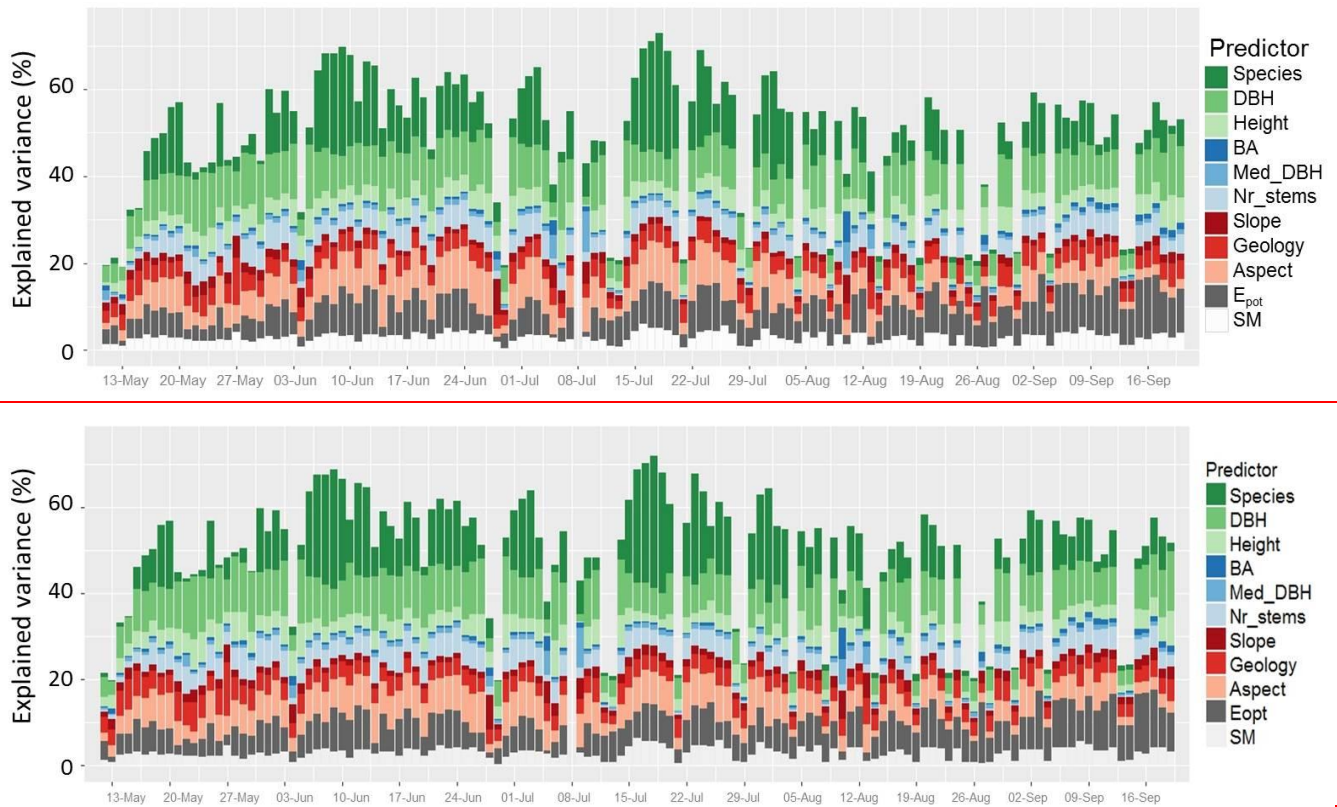

Figure 6: <u>**Proportion of variance explained by the different predictors in the**</u>~~Explained variance of~~ **daily linear models of spatial sap velocity patterns: 132 daily models from 61 trees at 24 sites.**
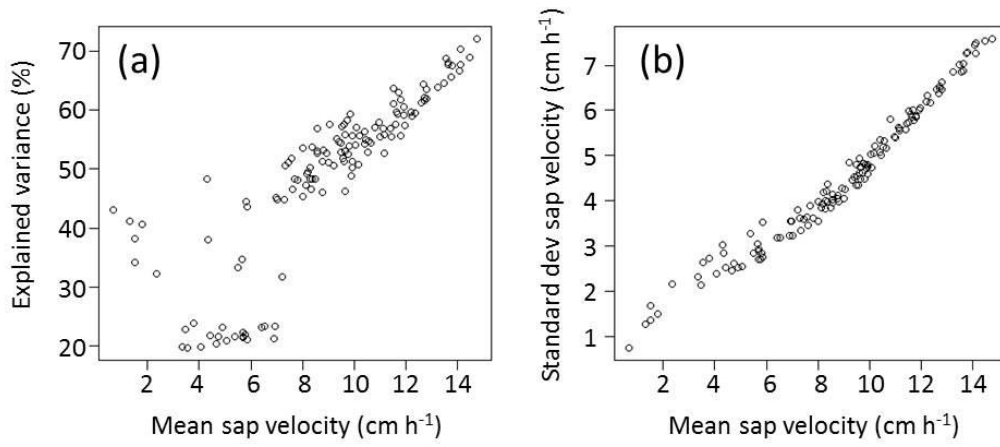
Figure 7: (a) Explained variance of the linear models in relation to mean sap velocities for all 132 days of the study period and (b) standard deviation of sap velocity depending on mean sap velocities for those 132 days.
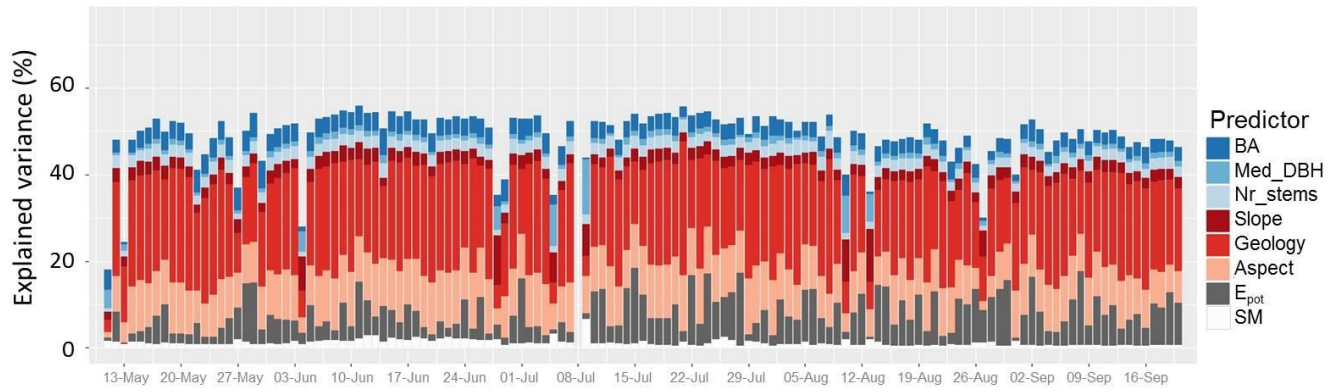
Figure 8: Proportion of variance explained by the different predictors in the daily linear models of spatial sap flow patterns: 132 daily models from 61 trees at 24 sites.
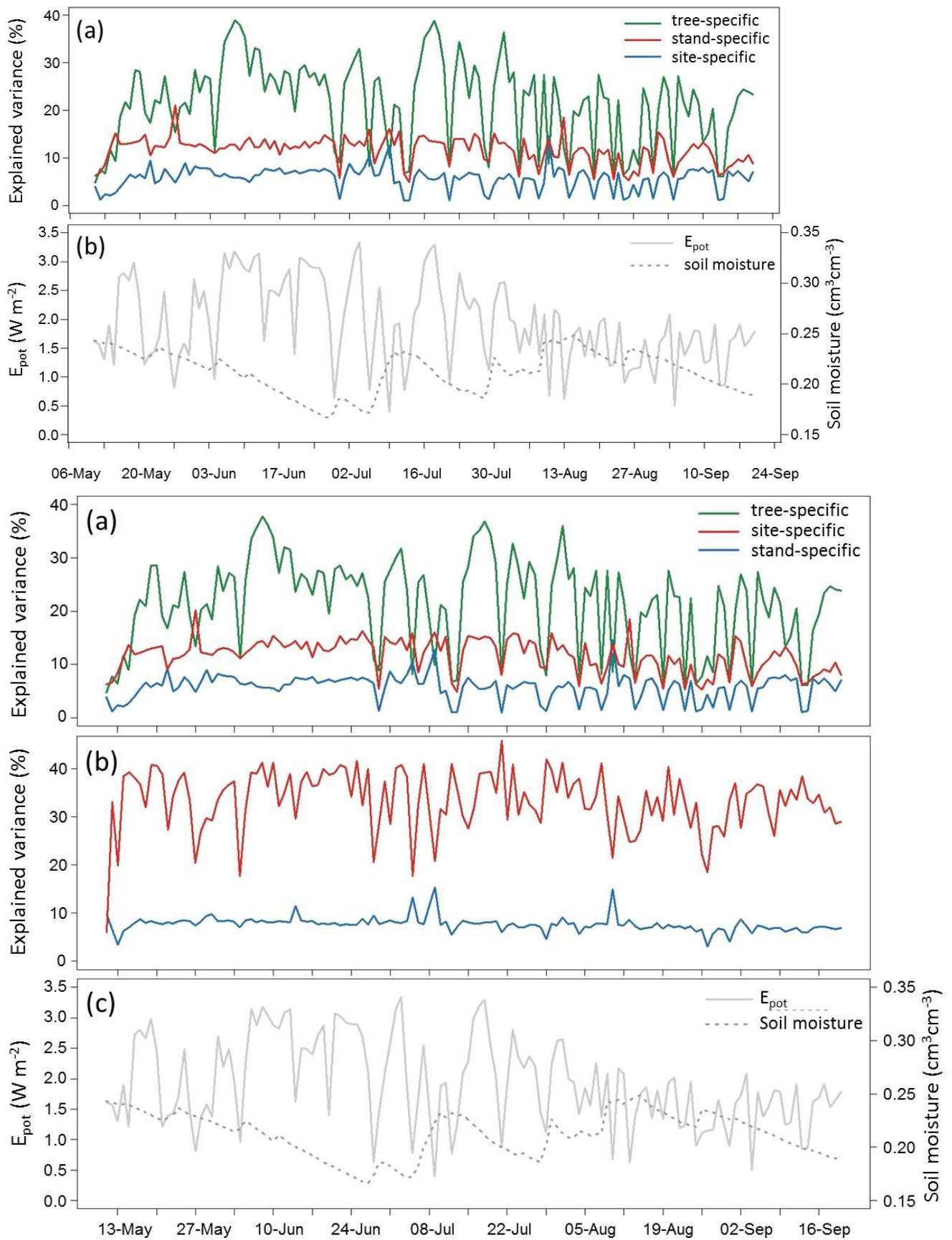
Figure 89: (a) Explained variance of the daily linear models, separated according to the predictor groups used in the regressiontree-, stand- and site-specific predictors, (a) for sap velocity and (b) for sap flow. (bc) Catchment average of soil moisture and potential evaporation E_{pot}.

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