1 Discussion

Climate change has decreased risk for all species across Central Europe. Our results integrate over the major geographical and climatic factors known to influence false spring risk. In line with previous work, our results support that higher elevations tend to experience more false springs (Vitasse *et al.*, 2018; Vitra *et al.*, 2017) and sites that are generally warmer have lower risks of false springs (Wypych *et al.*, 2016a). Individuals further from the coast typically initiated leafout earlier in the season, which subsequently lead to an increase in risk and, similarly, years with higher NAO indices experienced a slight increase in risk. But many of these factors have been re-shaped by climate change. Across species, we find that NAO and mean spring temperature have shifted the most after 1983, while the effect of distance from the coast has only shifted slightly and the effect of elevation has not shifted (Figure S2.)

These shifts in the influence of climatic and geographic factors in turn result in different effects of climate change on species. Though there has been a consistent decrease in false spring risk for all species we studied— given the combined effects of all factors that contribute to false spring risk—some species (e.g. *Fraxinus excelsior* and *Quercus robur*) have experienced total decreases while others have experienced smaller shifts in risk (e.g., *Aesculus hippocastanum*, *Alnus glutinosa* and *Betula pendula*.) These species-specific effects integrate over shifts in the influence of climatic and geographic factors on false spring risk, as well as residual variation not explained by these factors, suggesting for which species we have a robust understanding of what drivers underlie shifts in false spring risk with climate change, versus those species where more understanding is most critically needed.

Climatic and geographic effects on false spring risk

Past studies using single parameters for false spring events (Liu *et al.*, 2018; Ma *et al.*, 2018; Vitasse *et al.*, 2018; Vitra *et al.*, 2017; Wypych *et al.*, 2016b) have led to contradicting predictions in future false spring risk. By integrating both climate gradients and geographical factors, we were able to disentangle the major predictors of false spring risk and merge these with species differences to determine which factors have the strongest effects on false spring risk. Mean spring temperature, distance from the coast and climate change were the strongest predictors for false spring risk, however, NAO and elevation also affected risk, emphasizing the need to incorporate multiple predictors.

Since the onset of recent major climate change, the strength of these climatic and geographic effects have

₂₉ changed, highlighting the need to better understand and model shifting drivers of false spring. After climate

₃₀ change, our results show a large decrease in risk of false spring with higher NAO indices. This could be

₃₁ because high NAO conditions no longer lead to temperatures low enough to trigger a false spring—that is,

₃₂ with climate-change induced warming high NAO conditions may no longer produce the freezing temperatures

₃₃ needed for false springs. Conversely, we found an increased risk with warmer mean spring temperatures after

₃₄ climate change, which we suggest may be driven by our studied plant species responding very strongly to

₃₅ increased spring warming with climate change (i.e., large advances in spring phenology, Figure S1), which

₃₆ results in an increased risk of exposure to false springs at these locations. Clearly, improving mechanistic

₃₇ models of how warming temperatures affect budburst (Gauzere *et al.* (2017); Chuine *et al.* (2016)) could

₃₈ improve our understanding of how NAO and mean spring temperatures contribute to false spring risk.

₃₉ Variation in risk across species

₄₀ Due to the prominent shifts in the geographic and climatic factors (i.e., mean spring temperature, elevation,

₄₁ distance from the coast and NAO indices) with climate-change induced warming, there was a decrease in risk

₄₂ of false springs across all species after 1983. Though residual effects of climate change resulted in marked

₄₃ differences in risk between early- and late-leafout species. Before 1983, false spring risk was slightly higher for

₄₄ species initiating leafout earlier in the spring but overall the risk was more consistent across species (Figure

₄₅ **??**E). After climate change, however, the early-leafout species (i.e., *Aesculus hippocastanum*, *Alnus glutinosa*

₄₆ and *Betula pendula*) had an increased risk, the middle-leafout species—i.e. *Fagus sylvatica*—had a similar

₄₇ level of risk as before and the later-leafout species (i.e., *Fraxinus excelsior* and *Quercus robur*) had a slightly

₄₈ decreased risk (Figure **??**E). Further exploration of the possible climatic factors not included in the model

₄₉ (e.g., over-winter chilling temperature shifts) influencing this effect are necessary for forecasting.

₅₀ As seen by Figure **??**C species alone is not a sufficient predictor for false spring risk, especially when consid-

₅₁ ering the combined effects of all climatic and geographic factors coupled with climate change. Simply looking

₅₂ at the raw number of false springs for species suggests that *Fraxinus excelsior* and *Quercus robur* both had

₅₃ similar levels of false spring risk after climate change as before (Figure **??**C), however this conflicts with the

₅₄ overall model output (Figure **??**E). By additionally integrating climatic and regional factors—e.g., elevation,

₅₅ distance from the coast—we can unravel phenological effects on the probability risk from the climatic and

₅₆ geographic factors that contribute to an individual's level of false spring risk, which consistently decreases

₅₇ across species after climate change.

The overall ranges of the predictors are similar across species but *Betula pendula* extends to the highest elevation and latitude and spans the greatest range of distances from the coast, while *Quercus robur* experiences the greatest range of mean spring temperatures. Habitat preference and range differences among the species could also explain some of the species-specific variation in the results. Within our species, *Betula pendula* has the largest global distribution, extending the furthest north and east into Asia. The distribution of *Fraxinus excelsior* extends the furthest south (into the northern region of Iran). These range differences could underlie the unexplained effect of climate change seen in our results and why the shifts in climatic and geographic factors did not explain much of the variation in false spring risk across species. *Fagus sylvatica*) was better explained by the model and this species has a smaller range, more confined to Central Europe. Future research that captures these spatial, temporal and climatic differences across myriad of species would greatly enhance predictions and help us understand these residual effects of climate change.

Forecasting false springs

Our study shows how robust forecasting must integrate across major climatic and geographic factors that underlie false spring, and allow for variation in these factors across species and over time as warming continues. Of the five climatic and geographic factors we examined, only the effect of elevation remained constant before and after climate change. This is perhaps not surprising as climate change is shifting critical spring temperatures and reshaping the temporal and spatial dynamics of how climate effects budburst, leafout and freezing temperatures, yet it highlights the complexity that robust forecasting will require. Further, the differences we found across species suggest we can forecast some species better than others—such as *Fagus sylvatica*—which experienced almost zero unexplained climate change effects, thus, risk was likely determined by the climatic and geographic factors already included in the model.

Moving forward, more data on more species will be critical for estimates at community or ecosystem scales (at least in species-rich ecosystems). Related to this, more research on the effects of climate change on both budburst and leafout, the timing when individuals are most at risk to spring freeze damage (Chamberlain *et al.*, 2019; Lenz *et al.*, 2016) and on what temperatures cause leaf damage will help better understand differences across species. Though we found that differing rates of leafout across species had minimal effects on predicting risk, we did find that the lower temperature threshold can have an impact on model estimates (and thus forecasts), with lower temperature thresholds (i.e., -5°C versus -2.2°C) predicting increased risk across all six study species. Our study does not assess the intensity or severity of the false spring events

observed nor does it record the amount of damage to individuals. Other research has shown that this temperature threshold may vary importantly by species (Körner *et al.*, 2016; Lenz *et al.*, 2013; Zhuo *et al.*, 2018; Bennett *et al.*, 2018). Some species or individuals may be less freeze tolerant (i.e., are damaged from higher temperatures than -2.2°C), whereas other species or individuals may be able to tolerate temperatures as low as -8.5°C (Lenz *et al.*, 2016). Further, cold tolerance can be highly influenced by fall and winter climatic dynamics that influence tissue hardiness (**?**Vitasse *et al.*, 2014; Charrier *et al.*, 2011) and can also influence budburst timing (Morin2007). Thus, we expect these effects are likely integrated and that useful forecasting will require far better species-specific models of budburst, leafout and hardiness—including whether budburst and hardiness may be inter-related.

Climate change is complicating the influence of both climatic and geographic factors, magnifying species-level variation in false spring risk, plus we are still missing key components that explain this interspecific variation. Our study focuses on one region (i.e., Central Europe) with high-quality and abundant data and we hope that our results can be applied to other systems as more and more data becomes available. Integrating these findings into future models will provide more robust forecasts and help us begin to unravel the complexities of climate change effects across species.

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