Strong impact of temperature and resource specialisation on patterns of voltinism within an oak-associated insect community

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Abstract
1. Insect phenology consists of the timing of life events, as well as the number of generations (voltinism). While several studies have focused on the impact of climate on the timing of seasonal events, or the voltinism of single species, we have few insights into the factors that shape patterns of voltinism within ecological communities. Importantly, voltinism can have a major impact on population growth, species interactions, and rate of evolution.
2. We investigated the relative importance of spatial variation in temperature and species traits in shaping patterns of voltinism within an herbivore community feeding on deciduous oaks across a temperature gradient in Europe.
3. Voltinism increased with temperature, where the probability for a species to be univoltine decreased with temperature, whereas the probability for a species to be strictly multivoltine increased with temperature. The relative abundance of the first and subsequent generations of multivoltine species did not significantly change along the temperature gradient. Resource specialisation affected voltinism, where oligophagous and polyphagous species were more likely to be strictly multivoltine than narrow oligophagous species. Overwintering stage and body size did not affect voltinism, and there was no evidence that species traits influenced the relationship between temperature and voltinism.
4. Our findings highlight that temperature and species traits shape variation in voltinism within an herbivore community associated with oak trees. These temperature-induced shifts in voltinism within the oak-associated herbivore community may have profound effects on the synchrony within and between trophic levels, and consequently for food web structure and outbreak dynamics.

KEYWORDS
climate, herbivore community, Quercus, species traits, voltinism

INTRODUCTION
Spatial and temporal variation in climate can have a major impact on the phenology of organisms (Menzel et al., 2006; Parmesan, 2007). In temperate regions, temperature influences when plants and insects start growing or emerge in spring, when they reproduce, and when the activity ends in autumn (Bale et al., 2002). However, more radical changes than shifts in timing can happen with higher temperatures...
and longer growing seasons: insect species may increase the number of generations per year (voltinism) (Altermatt, 2010a; Parmesan, 2007). Changes in voltinism in response to spatial and temporal variation in climate may differ between species within ecological communities, for example, due to differences in species traits related to resource specialisation, overwintering stage or body size (Altermatt, 2010b; Hodkinson et al., 1998; Teder, 2020; Zeuss et al., 2017). Such variation among species in their relationship between temperature and voltinism may shift the synchrony within and between different trophic levels (Thackeray et al., 2016) and increase the frequency of outbreak dynamics (Isaev et al., 2018). Nonetheless, studies to date have mostly focused on the voltinism of single species (Lindstad et al., 2019; Stoeckli et al., 2012) or a broad range of insects originating from a wide variety of ecosystems (e.g., Altermatt, 2010a; O’Neill et al., 2012; Pöyry et al., 2011; Teder, 2020). Hence, we lack insights into the relative importance of climate and species traits on voltinism at the community level.

Voltinism of insects depends on environmental conditions (Bale et al., 2002; Lindstad et al., 2019) and species traits (Altermatt, 2010b; Hodkinson et al., 1998; Teder, 2020; Zeuss et al., 2017), and might differ across the phylogenetic tree as based on the underlying genetic background (Ahn et al., 2016; Lindstad et al., 2019; Marcon et al., 2003; Pruisscher et al., 2018; Stoeckli et al., 2012). Among the environmental conditions, photoperiod is known to affect insect emergence and diapause induction (Lindstad et al., 2019; Stoeckli et al., 2012). The developmental rate of lepidopterans depends on temperature (Bale et al., 1997, 2002; Hodkinson et al., 1998). Generally, insects develop faster with higher temperature, and are thus more likely to develop multiple generations in the parts of their range with higher mean temperatures and longer growing seasons (Bale et al., 1997, 2002; Hodkinson et al., 1998). Species that have a single generation in years with an average temperature may still develop an additional generation in years with higher temperature, a phenomenon often referred to as partial bivoltinism or partial multivoltinism (Porter et al., 1991; Pöyry et al., 2011; Van Dyck & Wiklund, 2002). Some species may develop more than one generation per year throughout their entire (or studied) range, often referred to as strictly multivoltine, while some other species develop only one annual generation throughout their range (strictly univoltine). Partially and strictly multivoltine species may show variation in the relative abundance between generations in response to climate. For example, Altermatt et al (2010a) showed that for 190 of 263 lepidopteran species in central Europe the abundance in the second and subsequent generations increased as compared to the first generation in response to increasing temperatures. Besides temperature and season length, variation in voltinism is also likely to depend on species traits like resource specialisation, overwintering stage or body size. For example, generalists can extend their growing season by feeding on alternative hosts in spring or autumn (Altermatt, 2010b), species that overwinter as an egg often start feeding earlier in spring (Svensson, 1993), and smaller species usually have shorter life cycles (Danks, 2006). Nevertheless, some spring feeding species might remain strictly univoltine, as they are specialised on developing leaves (Tammaru et al., 2001; Tikkanen & Paivi, 2002).

Species that share the same habitat (i.e., a community; Emlen, 1977) may respond differently to changes in temperature, which can have pronounced consequences at the community level, for example due to changes in plant-mediated (Denno et al., 1995; Kaplan & Denno, 2007) and natural enemy-mediated species interactions (Morris et al., 2004, 2014). Despite this, studies have either focused on the impact of spatial and temporal variation in temperature and photoperiod on the voltinism of individual species (e.g., Ahn et al., 2016; Lindstad et al., 2019; Stoeckli et al., 2012) or examined changes in voltinism across a broad range of insects originating from a wide variety of ecosystems (e.g., Altermatt, 2010a; Pöyry et al., 2011; Teder, 2020). While this has unambiguously demonstrated that species vary in how rapidly they change in voltinism in response to changes in climate, we lack insights into the consequences of changes in voltinism for species interactions within ecological communities. One area of particular interest is the northern range of the distribution of the community, where changes in voltinism in response to climate may be particularly pronounced due to low temperatures and a short growing season. Taken together, we need studies focusing on spatial variation in voltinism at the community level, by focusing on a set of species sharing the same habitat.

We investigated the impact of temperature (growing degree days above 5°C, GDD5) and species traits (resource specialisation, overwintering stage and body size) on patterns of voltinism in an herbivore community associated with a focal host plant. For this, we used citizen science data on the seasonal flight times of specialist and generalist lepidopterans feeding on deciduous oak across Europe. More specifically, we addressed three questions:

1. How does voltinism change with temperature across Europe? Are changes particularly pronounced at the northern limit of distribution of oak?
2. For multivoltine species, does the relative abundance of individuals in the first versus subsequent generations change with temperature?
3. What is the relationship between species traits (resource specialisation, overwintering stage and body size) and voltinism? Do species with different species traits vary in their response to spatial variation in temperature?

**METHODS**

**Study system**

We focused on the lepidopterans on deciduous oaks for three reasons: (i) deciduous oaks are widespread across Europe, (ii) the lepidopteran community associated with oak is highly diverse, and (iii) the oak-associated community has been extensively studied. The hybrid complex formed by deciduous oaks (i.e., *Quercus petraea* (Matt.) Liebl., *Q. pyrenaica* Willd. and *Q. robur* L.) is widely spread across Europe, with the southern limit of its distribution in the northern half of the
Species selection and grouping

In this paper, we focused on lepidopteran species feeding on deciduous oak across a latitudinal gradient in Europe. For this, we used citizen science data taken from the GBIF repository (GBIF.org, 2018). To construct our database, we included species that had at least 10 observations in one of six countries (Spain, France, Germany, the Netherlands, Denmark and Sweden) (cf. Altermatt, 2010a) during the period from 2003 to 2018. From this list (n = 260), we excluded species that overwinter as adults (n = 33) or are migratory (n = 2), because the last annual generation can be confounded with the first generation of the following year. The data set consisted of 184,682 records of the adult stage. Each individual record consisted of a species name, date (transformed to the Julian date) and coordinates.

To examine the relationship between voltinism and growing degree days above 5°C (GDD5), we took a three-step approach (for details on each step, see paragraphs below). First, as flight curves can only be calculated from a set of multiple observations for a given species, we subdivided the variable GDD5 into multiple classes. Second, we estimated the level of voltinism (univoltine, partially multivoltine, strictly multivoltine) from the flight curves using kernel density estimation, separately for each combination of species and GDD5 class. Third, we used the variable voltinism (as estimated separately for each combination of species and GDD5 class) within ordinal models that included the predictor GDD5, as well as three life-history traits. This approach was previously used to analyse changes in voltinism along a latitudinal gradient (Pöyry et al., 2011; Teder, 2020; Zeuss et al., 2017) and through time (Altermatt, 2010). To validate the robustness of the approach, we repeated the steps above for the predictor variable ‘latitude’ (see Data S1).

We extracted data on temperature from the ENVIREM database, which provides a set of climatic variables relevant for ecological and physiological processes (Title & Bemmels, 2018). To analyse the impact of spatial variation in temperature on voltinism, we extracted growing degree days above 5°C (GDD5) for the coordinates of each observation from the ENVIREM database (Title & Bemmels, 2018) for the period from 1960 to 1990, with a resolution of 20 km. ENVIREM calculates GDD5 values as the sum of mean monthly temperature for months with mean temperature greater than 5°C multiplied by the number of days in each month (Title & Bemmels, 2018). We subdivided GDD5 into multiple classes to allow the calculation of flight curves, which can only be constructed based on multiple observations. To allow robust statistical inference among classes, we subdivided GDD5 into four classes, with >100 species per class: (i) <20,000, (ii) from 20,001 to 25,000, (iii) from 25,001 to 30,000 and (iv) >30,000, where we selected the midpoint of each class to create the continuous response variable GDD5. To investigate the impact of spatial variation in temperature on voltinism at the northern range limit of the oak community, we used the following GDD5 classes: (i) <19,000, (ii) from 19,001 to 20,000, and (iii) from 20,001 to 22,000.

For each species, we defined the level of resource specialisation as based on the host plants used within Europe: (i) narrow oligophagous, if the species only feeds on plants within the Quercus genus, (ii) oligophagous, if the species only feeds on species within the Fagaceae, and (iii) polyphagous, if the species feeds on more than two plant families. We further recorded the overwintering stage (egg, larva or pupa) and body size (using male wingspan as a proxy; Jonko, 2019).

Assessing univoltinism and multivoltinism

To calculate voltinism for each combination of species and GDD5 class, we adapted the methodology from Altermatt (2010a), using kernel density estimates of dates of the records within each GDD5 class with the default function densityplot in R v. 3.5.0 (R Development Core Team, 2020). Kernel density estimation is a non-parametric way to estimate the probability density function of a variable (occurrence over time in our case) that can be seen as a smoothed line of a histogram, with the advantage that it is not necessary to define an arbitrary bin width. We used the default kernel-bandwidth, which is estimated from the data and is scale invariant (Altermatt, 2010a). Given a sample of individual flight records of a species, kernel density estimation extrapolates the individual data and predicts the flight period and relative occurrence of individuals of the entire population over the summer. We used the set of species that had a minimum of 10 individuals in at least two GDD5 classes. This cut-off level allowed us to compute a reasonable kernel-density estimate and at the same time avoided the exclusion of many species that are rare. Univoltine species will have a unimodal kernel-density distribution, while bivoltine species will have a bimodal distribution, etc. The species whose flight curve did not present local minimum values were classified as univoltine, while the rest were classified as multivoltine. To distinguish between strictly multivoltine and partially multivoltine species, we visually inspected each flight curve. Following Altermatt (2010a), we considered as strictly multivoltine species those that consistently present a clear bimodal distribution, while partially multivoltine species present small peaks in their flight period curves separated from the main one only in specific years (see Pöyry et al., 2011). As such, we obtained an estimate of voltinism for each combination of species and GDD5 class.
Assessing the relative population sizes in the first and subsequent generations of multivoltine species

For the multivoltine species, we estimated the magnitude of the second and subsequent generations relative to the first generation, separately for each combination of species and GDD5 class. Following Altermatt (2010a), we pooled the second and potential subsequent generations for the analysis. We defined the change between the first and the subsequent generations as the date at which the slope between the first two peaks of the kernel density curve was minimal. We calculated the area under the curve both to the left and to the right of the minimal value obtained for the x-axis, and calculated the relative proportion of the second and subsequent generations relative to the first generation. When this value is smaller than 1, the first generation is more abundant than subsequent generations, and a value larger than 1 indicates that the second and subsequent generations are larger than the first generation.

Statistical analyses

At the European scale, we used ordinal models to assess the impact of GDD5, resource specialisation, overwintering stage and body size on voltinism. For this, we modelled the voltinism of each species in each GDD5 class (1 = univoltine, 2 = partially multivoltine and 3 = strictly multivoltine) as a function of the fixed effects GDD5 (continuous), resource specialisation (categorical), overwintering stage (categorical) and body size (continuous). Note that the response variable voltinism has a single value for each combination of species and GDD5 class, as estimated from the flight curves. To examine whether species with different species traits varied in their response to GDD5, we included two-way interactions between species traits and GDD5. To account for phylogenetic relationships among species, we included family and genus as random effects. To account for species-level effects, we included species as a random effect. The continuous predictors GDD5 and body size were scaled to zero mean and unit variance. To assess whether latitude can be used as a proxy for GDD5, we also conducted a similar set of analyses where we included latitude instead of GDD5 (see Data S1 for a detailed explanation). We fitted the model using the function clmm in the R-package ordinal (Christensen, 2019; R Core Team, 2020), and tested for significance using the function Anova in the package car (Weisberg, 2019). We ran post-hoc analyses for significant categorical predictors by using the function lsmeans implemented in the R-package lsmeans (Lenth, 2016). For a detailed overview of the statistical models conducted, including questions, response variables, predictors and R-functions used, see Table S1.

To assess to what extent individual species increase, decrease or do not change their voltinism with GDD5, we modelled voltinism of each species in each GDD5 class (1 = univoltine, 2 = partially multivoltine and 3 = strictly multivoltine) as a function of GDD5. We ran the model using the function clm in the R-package ordinal (Christensen, 2019). We extracted regression slopes for each species, where positive slopes represented species that increased their voltinism with GDD5, negative slopes represented species that decrease their voltinism with GDD5, and slopes with a zero value represented species that were not affected by GDD5.

To investigate the impact of temperature on voltinism at the northern range edge of the distribution of oak in Sweden, we modelled the impact of GDD5 on voltinism, and – as we did at the European scale – assessed if individual species increase, decrease or do not change their voltinism with GDD5 (see Table S1 for a summary of models).

Finally, we investigated whether the relative proportion of individuals in the first and subsequent generations for a given species changed with GDD5 class. As the relative size of the different generations varies strongly among species, we used a paired Wilcoxon signed-rank test, where individual species were the unit of replication. In other words, we tested whether (across all species) the relative size of the different generations of each species was higher in one GDD5 class as compared with another GDD5 class. We conducted the Wilcoxon signed-rank test separately for each pairwise combination of GDD5 classes.

RESULTS

The impact of GDD5 on voltinism at the community level

The level of voltinism increased with temperature (Table 1 and Table S2, Figure 1), where the proportion of univoltine species decreased with GDD5 both in Europe and at the oak’s northern range edge in Sweden, while the proportion of strictly multivoltine species followed the opposite pattern (Figure S1). The proportion of partially multivoltine species did not change with temperature in either Europe or the oak’s northern range edge in Sweden (Figure S1). The relationships between the level of voltinism and latitude (as a proxy for GDD5) were similar to those for GDD5 (for details, see Data S1, Figure S2, and Tables S3 and S4). A large fraction of species within the lepidopteran community associated with oak increased their voltinism with GDD5, both in Europe and at the oak’s northern range edge in Sweden ($\chi^2_1 = 27.4, p < 0.001$ and $\chi^2_1 = 35.2, p < 0.001$; Figure 2).

The relative population sizes in the first and subsequent generations of multivoltine species

The relative size of the first and subsequent generations of multivoltine species was not significantly affected by GDD5 (for all pairwise comparisons, $p > 0.05$; Table S5).

The impact of species traits on voltinism

Voltinism was related to resource specialisation, with a higher level of voltinism for oligophagous and polypagous species than for narrow
| Predictor | Estimate | SE  | $\chi^2$ | df | $p$     |
|-----------|----------|-----|----------|----|---------|
| GDD5      | 0.44     | 0.09| 20.69    | 1  | <0.001  |
| Resource specialisation | |     |       |    |        |
|          |          |     |          |    |         |
|          |          |     |          |    |         |
| Overwintering stage | |     |          |    |         |
|          |          |     |          |    |         |
|          |          |     |          |    |         |
| Body size | 0.07     | 0.14| 0.91     | 1  | 0.34    |
| GDD5 × Resource specialisation | |     |          |    |         |
|          |          |     |          |    |         |
| Overwintering stage | |     |          |    |         |
|          |          |     |          |    |         |
|          |          |     |          |    |         |
| GDD5 × Overwintering stage | |     |          |    |         |
|          |          |     |          |    |         |
|          |          |     |          |    |         |
| GDD5 × Body size | −0.18    | 0.09| 3.81     | 1  | 0.05    |

Variance components

Family = 0.03
Genus = 0.21
Species = 1.51

Note: The response variable voltinism consisted of a single value for each combination of species and GDD5 class, as estimated from the flight curves. Shown are the results of ordinal models, including parameter estimates and their associated standard errors (SE), $\chi^2$ values, degrees of freedom and $p$-values. Significant $p$-values ($p < 0.05$) are shown in bold. Qualitative conclusions did not change when the model was simplified.

**Figure 1** The relationship among temperature (GDD5) and the level of voltinism (a) in Europe and (b) at the oak’s northern range edge in Sweden. Shown are linear trend lines with their associated standard error (shaded area) from the ordinal models.
oligophagous species (Figure 3a, Table 1 and Table S6). Body size and overwintering stage were unrelated to voltinism (Figure 3b,c, Table 1). Species with different life-history traits did not differ in their relationship between voltinism and GDD5 (Table 1).

DISCUSSION

We used citizen science data to disentangle the effects of temperature and species traits on patterns of voltinism within a community of lepidopterans sharing a single resource, the deciduous oaks. Voltinism increased with temperature across Europe and at the northern edge of the oak distribution in Sweden, where the proportion of univoltine species decreased with GDD5, while the proportion of strictly multivoltine species followed the opposite pattern. Yet, the relative abundance between the first and subsequent generations did not change across the temperature gradient. Among the species traits, only resource specialisation was related to voltinism, whereas overwintering stage and body size had no relationship with voltinism. The strong effect of spatial variation in temperature on the voltinism
within the lepidopteran community associated with deciduous oaks indicates that—with ongoing climate warming—the number of generations of many, but not all, species will increase. Still, the speed of such changes will depend on whether the underlying mechanism is phenotypic plasticity, or requires local adaptation, which might differ among species. Such changes in voltinism will have major consequences for levels of herbivory, the synchrony between host plants, herbivores and their natural enemies, and food web structure.

Voltinism increased with temperature across a latitudinal gradient within Europe and at the northern range edge of oak in Sweden. Our finding of an increase in voltinism across a temperature gradient in Europe matches two previous studies on patterns of voltinism at large spatial scales (Teder, 2020; Zeuss et al., 2017). Zeuss et al. (2017) demonstrated that lepidopterans and odonates increased their voltinism across a latitudinal gradient from 35°N to 70°N, and Teder (2020) reported that >50% of 731 investigated lepidopterans increased in voltinism along a 1.5°C temperature gradient. Species that remain univoltine are frequently strongly synchronised with their host plant and are potentially vulnerable to phenological mismatch with their host plants (Teder, 2020). These changes in voltinism are most likely linked to resources and time limitations, especially in northern areas, where the average temperatures are lower and the growing season is shorter (Altermatt, 2010a; Zeuss et al., 2017). Our findings of a clear relationship between voltinism and temperature at the northern range of the distribution matches a study by Pöyry et al. (2011), who found a positive relationship between voltinism and temperature for 178 lepidopterans along a latitudinal gradient of 1000 km in Finland (Pöyry et al., 2011). We observed similar changes in voltinism when using latitude as a proxy for temperature in the analyses, which matches with two previous studies that found similar patterns for temperature and latitude (Pöyry et al., 2011; Zeuss et al., 2017). Thus, we observed that patterns of voltinism are robust to the exact predictor variable chosen (GDD5 and latitude), and further validates the use of latitude as a proxy for temperature. From a methodological perspective, we note that the construction of flight curves from data accumulated across multiple years in this and previous studies (Altermatt, 2010a; Altermatt, 2010b; O’Neill et al., 2012; Pöyry et al., 2011; Teder, 2020; Zeuss et al., 2017) could, in some cases, cause misinterpretations. For example, large temperature variations across years could obscure multivoltine patterns by the appearance of a single flight peak, and, conversely, create multiple peaks for univoltine species. Our database was constructed based on citizen science data, which has its own limitations (no systematic sampling through space and time), which might explain the considerable number of species that had negative slopes for the relationship between voltinism and GDD5 (Figure 2). For example, species with little interest for amateur entomologists might be underrepresented. We hope that future studies, that for example use a massive sampling of a targeted community for multiple years, could directly address the nature and extent of such misinterpretations. One interesting avenue of study is also to examine whether the observed shifts in voltinism are the product of local adaptation or phenotypic plasticity, for example through a combination of observational studies on patterns of voltinism and the rearing of a broad set of species under a set of experimental temperature regimes (Coelho Jr & Parra, 2013; Lindestad et al., 2019; Pöyry et al., 2011; Tamiru et al., 2011; Teder, 2020).

While voltinism increased with temperature, we did not find a change in the relative abundance of the first versus subsequent generations for the multivoltine species within the lepidopteran community on oak. This contrasts with the only previous study that investigated changes in the relative abundance between the first and subsequent generations (Altermatt, 2010a). Altermatt (2010a) found that the relative abundance of the second and subsequent generations increased (as compared to the first generation) after 1980, which was attributed to climate change. One explanation for an increase in the relative abundance of the second and subsequent generations through time, but not in space, may be that natural enemies of the lepidopterans do not show the same rapid temporal response to climate change, whereas they have caught up in space. One methodological issue might also obscure some of the spatial patterns in the relative abundance of the first and subsequent generations: if light trapping is used to catch some of the lepidopterans, the capture efficiency decreases during the short nights in early summer, and particularly so in northern Europe. Overall, we hope that future studies will assess the generality of the role of temperature on the relative abundance of the first vs. subsequent generations across multiple geographical areas, and include multiple trophic levels to test for the role of synchrony between herbivores and their natural enemies in shaping these patterns.

Among the species traits, only resource specialisation showed a direct relationship with voltinism, and there was no evidence that species traits influenced the responses of species to temperature. For resource specialisation, oligophagous and polyphagous species were more likely to be multivoltine than narrow oligophagous species. Our findings match with Altermatt (2010b), who found that species with a broader host range are more likely to be multivoltine. Species that feed on multiple plants are not restricted to the availability of leaves of a single species, and can thus take advantage of a larger part of the growing season. The absence of a relationship between voltinism and overwintering stage or body size contrasts with previous studies which found that species that overwinter as pupa are more likely to develop multiple generations (Teder, 2020) and that voltinism decreased with body size (Teder, 2020; Zeuss et al., 2017). These discrepancies suggest that the relationships between species traits and voltinism might not be consistent among different ecological communities. Importantly, we found that species with different levels of resource specialisation, overwintering stage or body size did not differ in their relationship between voltinism and temperature. While there are no comparable studies, we tentatively conclude that the impact of temperature on voltinism is independent of these three species traits. Future studies might also investigate whether other traits influence the relationship between voltinism and temperature. For example, some species on oak, such as Epirrita autumnata and Operophtera brumata, are highly specialised on young expanding leaves in the early season (Tammaru et al., 2001; Tikkanen & Paivi, 2002), and the
occurrence of multiple generations in response to higher temperatures might thus be strongly selected against.

Overall, our findings demonstrate that temperature and resource specialisation have a strong impact on patterns of voltinism within a community of herbivores sharing a single resource, the deciduous oaks. Still, there is much variation among individual species, and we could predict the responses of individual species to temperature based on the life-history traits studied (i.e., resource specialisation, overwintering stage and body size). The overall pattern of increased voltinism with increasing temperature might result in higher levels of herbivory, increased population growth, and more rapid evolutionary responses, even though an increase in voltinism can also result in higher mortality rates if the final generation cannot successfully develop (i.e., the ‘developmental trap’; Pöyry et al., 2011, Van Dyck et al., 2015, Teder, 2020). The large variation among individual species within the same community indicates that species will respond at different rates (or not at all) to climate change, which may shift the synchrony within and between trophic levels, and thereby change food web structure and increase the likelihood of outbreak dynamics.

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DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

Data S1 Supporting information.

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