Ecological Entomology (2021), DOI: 10.1111/een.13015

On the role of direct sunlight for egg-laying behaviour: lessons and ideas from the speckled wood

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Abstract. 1. Butterflies rely on suitable weather conditions for thermoregulation during active behaviour. While non-sunny conditions are known to reduce time spent in active flight, detailed behavioural data on how variable microclimatic conditions affect decision making in specific behavioural contexts (e.g. habitat exploration, dispersal, mating, basking, oviposition) is often lacking.

2. We addressed the influence of direct sunlight on females of the speckled wood butterfly (*Pararge aegeria*) that were motivated to oviposit. To test this, we observed gravid butterflies one by one in (1) a cage within a greenhouse, where temperature was kept high all the time, and (2) an outdoor cage under uncontrolled weather conditions.

3. Our results show that butterflies almost exclusively oviposit under direct sunlight. Surprisingly, results were similar in the warm within-greenhouse cage, where activity remained high but oviposition never occurred during fully clouded conditions.

4. These results suggest that ovipositing butterflies require sunlight not only for thermoregulation. We hypothesise that direct sunlight benefits the ovipositing female by exposing more clearly the microclimatic variation of potential oviposition sites in the herbaceous layer of the vegetation. Heliophily during oviposition and pre-oviposition exploration may apply to a range of microclimate-sensitive species, particularly those living in microclimatically heterogeneous habitats. This warrants novel sensory ecological research, which will further improve our understanding of insect functional habitats.

Key words. Butterflies, oviposition site selection, sensory ecology, thermoregulation, weather conditions, woodland.

Introduction

Oviposition site choice is a critical component of the life history of an oviparous organism, including insects, as the decision on where to lay eggs has direct fitness consequences for both the egg-laying female and the offspring (Resetarits, 1996; Doligez & Boulinier, 2008). It is a critical ecological relationship between the organism (either as adult or egg) and the environment. Several field studies have characterised oviposition preference based on egg distribution patterns (Rausher *et al.*, 1981; Grossmueller & Lederhouse, 1985; Bonebrake *et al.*, 2010). However, there is still much to learn about the mechanisms involved in selecting and avoiding oviposition sites.

Oviposition site selection will affect, and in some cases largely determine, the developmental environment of the offspring. Therefore, it can be seen as a key maternal effect, particularly in rapidly changing landscapes (Gibbs & Van Dyck, 2009). Here, we addressed the role of direct sunlight for butterfly oviposition, including pre-oviposition, host plant search behaviour. Adult butterflies are diurnal and are heliothermic meaning they obtain the body heat required for flight activity from basking in the sun (Dennis, 1993). By adjusting their behaviour (including body position, basking frequency, and microhabitat selection), butterflies are able to regulate their body temperature within a range that is physiologically suitable for active flight (Clench, 1966; Wasserthal, 1975). Consequently, weather conditions strongly constrain the time window in which butterflies are fully active (Dennis, 1993; Cormont *et al.*, 2011). Sunny weather conditions, particularly in combination with low wind velocity (i.e. low levels of convective cooling), will facilitate longer periods of flight as well as longer individual flight bouts, more frequent access to nectar as fuel for flight and egg production (e.g. Hern *et al.*, 1996; Saastamoinen & Hanski, 2008). Under suitable

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weather conditions, females have more time for searching and evaluating multiple host plants to spread their eggs.

The role of sunlight is, however, not limited to thermoregulation only as it also triggers and affects other behaviours and behavioural performance levels. Examples include the induction of activity/sleep cycles (Helfrich-Förster, 2018), navigation during migration (e.g. sun compass in Monarch butterflies; Mouritsen & Frost, 2002), barrier to maintain butterfly community stratification near rain forest edges (de Vries, 1988), mate recognition, and selection as well as the induction of courtship behaviour (e.g. Obara & Hidaka, 1968; McDonald & Nijhout, 1996), among others.

Our study focused on the role of exposure to direct sunlight for oviposition in the Speckled wood butterfly (*Pararge aegeria*). *Pararge aegeria* is a woodland (edge), shade-tolerant species, which lays eggs on various grass species (Poaceae) in or close to woodland (Shreeve, 1986; Warren, 1987; Karlsson & Van Dyck, 2005).

Assuming the oogenesis-flight syndrome (i.e. trade-off between energy used for flight versus egg laying), female flight activity is expected to be more frequently constrained by weather conditions than is male flight activity (Pivnick & McNeil, 1986; Tigreros & Davidowitz, 2019). Females are more likely to avoid flight under suboptimal thermal conditions, as has been shown experimentally in *P. aegeria* (Merckx *et al.*, 2006). Therefore, thermoregulation and thermal conditions are predicted to play an important role for understanding the relationship between sunlight conditions and pre-oviposition behaviour. Our previous field observations show that females never oviposited under fully clouded conditions and similar observations have been reported by another expert (Shreeve T., pers. comm.). Nevertheless, when ambient temperatures are sufficiently high, females are capable of active flight under cloudy conditions (Wickman & Wiklund, 1983). This raises the notion whether direct sunlight is a prerequisite, or at least of particular significance, for oviposition in *P. aegeria* females.

In a first experiment, we created a setting where varying levels of sunshine and cloudiness were independent from its co-varying thermal effects. This way, we could test for oviposition behaviour under controlled, warm conditions suitable for flight activity, also in the absence of direct sunlight. Gravid, laboratory-reared F1-females were released one by one in a cage (provided with host plants and surrounding habitat elements) within a greenhouse. We then tracked each individual separately and recorded all behaviours observed. If sunlight indeed proves important during oviposition and pre-oviposition behaviour or *P. aegeria*, we hypothesise that females will not or rarely oviposit when the sky is fully clouded, even at high enough temperatures.

In a second experiment the year after, we tested whether there would be similar heliophilic tendency during oviposition behaviour while being in a more ecologically realistic setting. Observations were performed according to a similar observational procedure, but in a large outdoor cage at a woodland edge. This time, cloudiness was also registered during every oviposition bout.

Material and methods

Study species

The Speckled wood (*Pararge aegeria* L.) is a frequently used species for the study of ecology and evolution in insects (Watt & Boggs, 2003). This woodland and woodland edge butterfly is widespread throughout Europe (Kudrna *et al.*, 2011; Schneider *et al.*, 2021) and in the majority of its range, it flies in two, or even more, generations a year depending on its flexible life cycle regulation (e.g. Wiklund & Friberg, 2011). Several aspects of its thermal biology have been studied in detail, including habitat use (Schweiger *et al.* 2006), flight performance (Berwaerts & Van Dyck, 2004; Merckx *et al.*, 2006), temperature-dependent fecundity (Karlsson & Van Dyck, 2005), and male mate-locating behaviour (Shreeve, 1987). For previous work on egg laying in *P. aegeria*, we refer to Wiklund (1984), Shreeve (1986), Gibbs *et al.* (2005), and Gibbs & Van Dyck (2010).

Sampling and breeding

Both the outdoor and indoor experiment utilised F1-offspring of wild-caught gravid females originating from various populations in Belgium (i.e. Aalst, Brussels, Leuven, Herentals, Tienen, Leuven, Chaumont-Gistoux, Charleroi and Namur). All females were kept under the same laboratory conditions (temperature day/night: 23 °C/16 °C; photoperiod light/darkness: 16 h/8 h; lamps that simulated the solar light spectrum: Philips HPI-T Plus 400W/645). In their individual cage, females had access to artificial nectar on cotton (i.e. 20% honey solution) and a tuft of potted host grass for egg laying (i.e. mixture of *Lolium perenne* and *Poa pratensis*). From each female's brood, we transferred groups of 5 s-instar, full-sib larvae together on a new tuft of potted host grass. Pupae were placed individually in plastic cups until adult eclosion. Two to three days after eclosion, females were allowed to mate in a small cage (0.3 m × 0.3 m × 0.3 m) in which they stayed for 24 h. Next, females were kept at lower temperature (temperature day/night: 14 °C/12 °C) in a Sanyo incubator to reduce activity and energy expenditure. Still, temperature was high enough to not hinder development of the eggs (Berger *et al.*, 2008). They were kept under these conditions for at least 3 days allowing full egg maturation (Karlsson, 1987).

Indoor experiment: oviposition during thermally controlled conditions

During the late summer of 2018 (August–October), we installed a cage within a large compartment of a greenhouse at our university campus (see Fig. S1a, b). The cage in the greenhouse was an experimental arena, which consisted of four tunnels that were connected in a cross shape (GardenSkill Ltd growing tunnels for gardening; 3 m × 1.5 m × 1.5 m). The tunnels were made from carbon fibre rods and covered by polypropylene 4 mm insect netting. In the tunnels, we placed

several potted host grasses (*L. perenne* and *P. pratensis*) and background vegetation to simulate woodland conditions (e.g. with *Crataegus laevigata* trees). Grass was present in both shaded and sunlit places. Ambient temperature remained at an average (±SD) of 25.0 ± 2.9 °C and humidifiers were used to avoid low humidity levels.

The observer (SB) observed all individuals through live focal observations using open-source logging software BORIS (Friard & Gamba, 2016). With this programme, the user first sets an ethogram that may include both event and state behaviours, coded by assigning unique keyboard keys to them. Females were introduced individually. Both activity levels (i.e. proportion of time spent in flight or walking on surface) and oviposition probability (i.e. when the butterfly laid one or multiple eggs during a single observation) were registered.

Prior to each observation, we measured: ambient temperature, relative humidity, and degree of cloudiness (four-level scale: 0 = open sky; 1 = less than 40% clouds; 2 = more than 40% clouds; 3 = fully clouded). For the statistical analysis (see below), we compared the lumped categories 0–2 (sunny to partly clouded) with category 3 (fully clouded). When sunny to partly clouded, the experimental arena was at minimum exposed for a brief moment of direct sunlight during an observation. When 'fully clouded', the experimental arena was never exposed to direct sunlight. Each of the 58 females was individually released in the central part of the arena and observed for 20 min; for each individual, we conducted three release-and-observe trails spread over two consecutive days and completed 173 observation sessions in total.

Outdoor experiment: oviposition in ecologically representative conditions

During the late summer of 2019 (August–October), an outdoor cage (15 m × 4.20 m × 3 m) was set up, located at a forest edge nearby the university campus (Louvain-la-Neuve; see Fig. S1c, d). The frame of the cage consisted of steel tubes used for greenhouse construction (brand: Filclair). The frame was covered by black multifilament netting with 7 mm mesh size. The cage location was selected under assumptions of suitable oviposition conditions for *P. aegeria*. Suitability of habitat was later confirmed, as wild *P. aegeria* females were observed exploring outside the cage during observations. In the cage, different suitable host grass species (*Poa pratensis*, *Lolium perenne*, *Agrostis capillaris*, and *Holcus lanatus*) were naturally growing under a diversity of microhabitats characterised by different plant heights, levels of light penetrance, canopy cover, and object proximity (e.g. cage frame, netting, other obstacles). As in the indoor experiment, females were introduced individually in the cage and observed under the same observational protocol as the indoor experiment. Aside from registering weather conditions before the start of an observation, we also noted whether oviposition occurred during full sun exposure or not. Observation sessions lasted for 30 min and, when conditions were suitable, a female was observed for a second session later that day. In total, 84 sessions were conducted on a sample of 46 individual females.

Statistical analyses

For the indoor experiment, the probability of oviposition was tested with generalised linear models with oviposition probability as the binomial response variable using R 3.5.0 (R Core Team, 2018). Main effects of the model output are presented as Sums of Squares Type III using the Anova function from the 'car' package (Fox & Weisberg, 2019). Although temperature variation was limited in our greenhouse setting, we first verified for additional temperature effects (i.e. separate glm-model for oviposition probability with temperature as the only fixed effect). The output of this model allowed us to exclude temperature outliers (see Results) and hence, we were able to test the effect of cloudiness with the temperature-adjusted dataset. We used backward selection to reduce the full model based on the Akaike information criterion (AIC) estimate generated for each model output (Zuur *et al.* 2009). The most informatieve glm model (i.e. minimum AIC) did not include 'trial' (1, 2, or 3) and analysed 'oviposition probability' relative to 'cloudiness' (2 categories) as the only fixed variable.

For the outdoor experiment, the percentage of butterflies that oviposited under cloudy conditions was calculated. Here, only observations during which the sky was partly to fully clouded were used, since we wanted to test whether *P. aegeria* would oviposit when the sun is blocked by clouds.

Results

Indoor cage experiment

Despite efforts of controlling for temperature, we did find a positive effect of temperature for oviposition rate ($\chi^2 = 4.41$, df = 1, $P = 0.036$). This was due to low occurrence of oviposition at temperatures below 25 °C (see Fig. S2). Once observations at a temperature lower or equal to 25 °C (i.e. 35 of the 179 observations) were excluded, no temperature effect was found ($\chi^2 = 0.54$, df = 1, $P = 0.46$); we, therefore, continued analysis with this sub-dataset.

In the indoor experiment, the probability of oviposition was higher under sunny or moderately clouded conditions compared with observations under full cloudiness ($\chi^2 = 8.82$, df = 1, $P = 0.0030$). Although the clouded warm conditions appeared favourable for flight in females, no eggs were laid when the sky was fully clouded, while oviposition occurred in 20% of the observations when sky was not fully clouded during an observation (0/22 vs. 23/116; see Fig. 1).

Moreover, females did not become less active with increasing cloudiness. Surprisingly, the proportion of time spent active increased ($\chi^2 = 4.55$, df = 1, $P = 0.030$; 7% more active when sky was fully clouded, compared when only partly clouded or clear sky; see Fig. S3).

Outdoor cage experiment

During observations that included both clouded and sunny periods during a single observation, only 3% of the oviposition bouts occurred when clouds were in front of the sun (i.e. one

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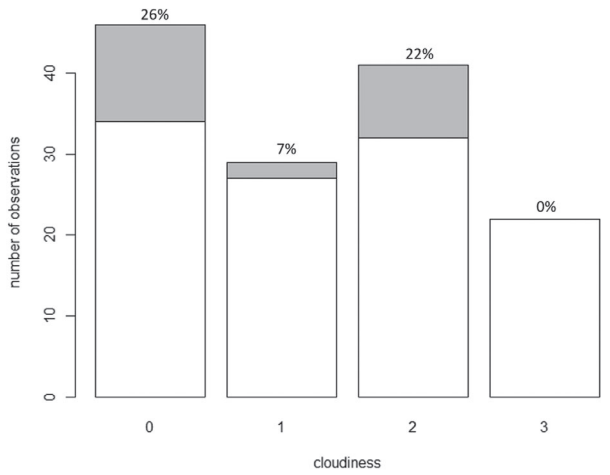


Fig. 1. Oviposition per level of cloudiness in indoor experiment. Number of 20-min observations is presented for each category of cloudiness (0 = open sky; 1 = less than 40% clouds; 2 = more than 40% clouds; 3 = fully clouded). In grey are the observations where one or more oviposition bouts occurred.

out of the 37 oviposition bouts of 29 different individuals). This oviposition bout occurred at relatively low ambient temperature (see Fig. 2). On two other occasions, butterflies stopped laying eggs during an oviposition event when clouds moved in front of the sun. On 6% of the observed oviposition bouts females laid eggs on sites that were shaded by vegetation or nearby objects, while the sun was shining. In total, 74% of the females oviposited during observation.

Discussion

Our outdoor cage results confirmed that Speckled wood females were reluctant to oviposit when direct sunlight was blocked by clouds. Oviposition does occur in sites that are locally shaded by cage object or vegetation, but still the oviposition behaviour was discouraged by the absence of direct sunlight at a wider scale. Such dependence has been related to thermal conditions and constraints (Shreeve, 1984). However, our results on egg-laying behaviour in the greenhouse setting provided a unique opportunity to separate the intertwined effects of direct sunlight radiation on the one hand and of sufficiently high ambient temperature on the other. In the greenhouse setting, oviposition did not occur under cloudy, but equally warm conditions. This effect was not confounded by a decrease of overall butterfly activity. Females continued flight activities under warm, but fully clouded, conditions.

The combination of our outdoor and greenhouse observations raises the question on the significance of sunlight during pre-oviposition in this butterfly. The opportunity to bask, and hence to thermoregulate behaviourally, cannot fully explain the role of direct sunlight for oviposition. Therefore, adapted experiments to explore a different or at least complementary role of direct sunlight are now warranted.

We suggest that sunshine during oviposition and pre-oviposition exploration increases the ability of Speckled wood females to better sense microclimatic variation, and therefore, microhabitat conditions suitable for egg laying. Our argument is twofold. First, sensing microclimatic variation is likely to be important for egg-laying Speckled Woods as they are considered to be adapted to structurally complex habitats with small-scale mosaics of different microclimates (Schweiger *et al.*, 2006; Pincebourde *et al.*, 2016). Larval survival strongly depends on the microclimatic buffering capacity of the selected oviposition site (Shreeve, 1986; Pateman *et al.*, 2016). Second, during sunlit conditions, sites that are characterised by a buffered microclimate are better detectable, since temperature differences between below- and above shade-casting vegetation are better amplified under direct sunlight (Morecroft *et al.*, 1998). Therefore, we predict that Speckled wood females time their egg-laying during direct sun exposure when detection and evaluation of microclimatic conditions are assumed to be more efficient.

We argue that besides hygro- and thermosensing, vision will also help females to detect suitable microclimatic properties. The habitat-specific natural light environment is a vital aspect in the behavioural ecology of butterflies, as they strongly depend on and anticipate particular light conditions to navigate, avoid predators, reproduce, and forage (Seymoure, 2018). The connection between light cues and small-scale mosaics of different microclimates is clearly demonstrated in below-canopy woodland habitats, where light intensity and spectral composition varies considerably. Light contrasts created by canopy 'gaps' or forest edges indicate sites exposed to higher amounts of solar heating (Endler, 1993; Davies-Colley *et al.*, 2000). In the context of detecting visual cues, direct sunlight is crucial, since contrasts in spectral composition (but not so much intensity) are much more pronounced under direct sunlit conditions than they are under cloudy conditions (Endler, 1993).

There is another line of circumstantial evidence, which comes from the well-studied male mate-location behaviour in Speckled woods. The extent of sunlight heating and the spatial configuration of sunlit spots on the forest floor through sunbeams shining through the canopy strongly affect male mate locating behaviour (Wickman & Wiklund, 1983; Van Dyck & Matthysen, 1998; Vande Velde *et al.*, 2011). Males adopting territorial perching to locate females will monopolise a sunlit patch at the forest floor. If the sun disappears after the clouds for longer than a few minutes, males retreat into the canopy (Van Dyck *et al.*, 1997). Once the sun is back, they return to their sunlit patch, which is accompanied by conflicts over residence (Davies, 1978; Wickman & Wiklund, 1983). Settlement of residency on sunlit patches has been suggested to relate to asymmetries in body temperatures between males on the sunlit hotspot and males passing by (Stutt & Willmer, 1998). However, elegant experiments by Kemp and Wiklund (2004) ruled out this interpretation. Follow-up experiments showed evidence of the role of light conditions for visual mate detection in *P. aegeria* (Bergman & Wiklund, 2009). Hence, also in females, we should not restrict the explanatory framework to their own body thermoregulation only.

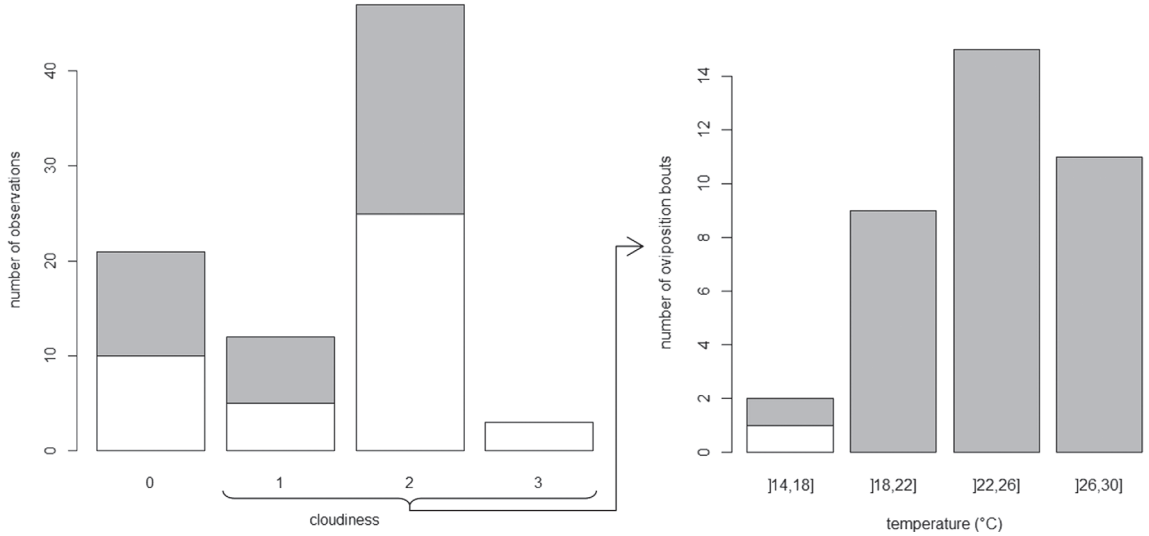


Fig. 2. Oviposition per level of cloudiness in outdoor experiment. Left: number of observations for each category of cloudiness (0 = open sky; 1 = less than 40% clouds; 2 = more than 40% clouds; 3 = fully clouded), recorded the beginning of each 30-min observation. In grey are the observations where one or more oviposition bouts occurred. Right: Number of oviposition bouts categorized by temperature category. In grey are all oviposition bouts that occurred while the sun was shining (yes), in white when the sun was blocked by clouds.

To the best of our knowledge, the timing of oviposition events during periods with direct sunlight as to facilitate microclimate detection has rarely been proposed in the literature, since studies on butterfly oviposition, and more generally on adult behaviour, are usually biased towards suitable weather conditions (Pollard, 1977; but see: Kobayashi, 1966; Williams, 1981; Grossmueller & Lederhouse, 1985). Such bias hinders our full ecological understanding of habitat use, including under conditions that deviate from optimal weather conditions (e.g. Dennis & Sparks, 2006). Therefore, observations of butterfly activity during cloudy but warm conditions are equally valuable.

Our experiments and suggestions indicate that more work is needed on the sensory ecology of butterflies and other insects in order to better grasp the complex ways they interact with the microclimatic heterogeneity for oviposition. There is growing interest in quantifying microclimates in woodlands and hedgerows (e.g. Vanneste *et al.*, 2020; Zellweger *et al.*, 2020), but it is warranted testing how organisms perceive such environmental variation as it ultimately turns structural habitats into functional habitats (Van Dyck, 2012).

Acknowledgements

This study was funded by an FRIA PhD grant of the Walloon Fund of Scientific Research F.R.S.-FNRS to SB and a research grant (ARC-grant 17/22-086 of Fédération Wallonie-Bruxelles and UCLouvain) to HVD. Thanks to T. Merckx, A. Kaiser, and S. Deconinck for their help with butterfly catching, to C. Pels, L. Ferrais, and D. Ozturk for helping with butterfly rearing and to M. Van der Borght, M. Migon, M. Pirnay, B. Ferauge, and D. Angelot for technical or administrative support. Thanks to L. Gregory for providing the photo in the graphical abstract. Thanks to T. Shreeve for contributing on the interpretation of the results and sharing personal experience in the field.

This is publication BRC 274 of Biodiversity Research Centre (ELIB/ELI/UCLouvain).

Author contributions

All authors co-designed the study. Both authors prepared the experiment. S.B. collected and analysed the data in interaction with H.V.D. S.B. wrote the first draft of the paper in close collaboration with H.V.D. Both authors discussed the results and contributed critically to the final manuscript. Both authors gave final approval for publication.

Data availability statement

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

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Observation cages. (a and b) Exterior and interior of the cage construction that was constructed within a greenhouse. (c and d) Exterior and interior of the outdoor cage, constructed near a forest edge.

Fig. S2. Oviposition success in the indoor experiment. Number of observations where oviposition occurred (grey) or not (white),

presented for each category of temperature in which these observations were performed

Fig. S3. Butterfly activity in the indoor experiment. The y-axis represents the proportion of time spent active throughout one observation and is presented for each category of cloudiness (0 = open sky; 1 = less than 40% clouds; 2 = more than 40% clouds; 3 = fully clouded).

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Accepted 11 January 2021

Associate Editor: Niklas Janz

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