Why and How to Create Nighttime Warming Treatments for Ecological Field Experiments

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While average global temperatures are increasing, a disproportionate amount of warming can be attributed to increasing nighttime temperatures rather than increasing daytime temperatures. Theory predicts that the timing of warming can generate different effects on organisms and their interactions within ecosystems. This occurs because an organism’s response to warming depends on the current temperature. For example, warming when temperatures are low may have positive effects on an organism, while warming when temperatures are already high may have negative effects on an organism. Most field experiments that examine the ecological effects of climate warming employ warming methodologies that disproportionately elevate daytime warming treatments. The bias towards daytime warming treatments may arise because daytime temperatures can be manipulated with relatively simple and inexpensive technology that capitalizes on solar energy, such as open-top chambers that create a “greenhouse effect” or shade structures that reduce temperatures. However, these popular methods are ineffective when solar radiation is absent, and thus do not create warming treatments that accurately mimic the temporal patterns of climate warming. To encourage the investigation of nighttime warming’s effect on ecosystems, we discuss why daytime and nighttime warming may have different effects on organisms, then present a review of methods that can be employed to elevate nighttime temperature in terrestrial field experiments. For each method, we offer a brief explanation, an evaluation of its pros and cons, and citations for further reference, as well as empirical data when possible. While some are impractical, we attempt to provide a comprehensive list of potential nighttime warming methods in hopes of stimulating ideas and discussions.

INTRODUCTION

Atmospheric carbon dioxide (CO₂)† concentrations have been increasing rapidly since the invention of the combustion engine in the 19th century and the subsequent global dependency on fossil fuel [1,2]. In 2016, atmospheric CO₂ concentrations surpassed 400 parts per million, a level which had not been experienced since the time early human ancestors diverged from old world monkeys [3]. These elevated concentrations of CO₂ and other greenhouse gases have increased radiative forcing in the atmosphere [4], resulting in more solar radiation being retained near the earth’s surface. As a consequence, global temperatures have been increasing at an unprecedented rate and are expected to continue to increase indefinitely [3].

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†Abbreviations: CO₂, carbon dioxide; TPCs, thermal (or temperature) performance curves; OTCs, open-top chambers.

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Although there is a global trend of increasing temperatures, more nuanced analyses reveal temporal variation in patterns of warming that may have important biological implications. Long-term datasets and climate change models have demonstrated seasonal variation in warming, with winters warming more than summers, as well as daily variation, with nighttime warming more than daytime [5-8]. Thus, within the growing season that supports much of the plant (including agriculture) and arthropod diversity in temperate, terrestrial ecosystems, daytime temperatures are not increasing dramatically. Instead, nighttime temperatures are becoming “less cool,” which results in an increase in average temperature [9-11].

To understand how and why the timing of warming might be important, we must first understand why we expect warming to affect organisms in general. Temperature affects organisms directly (e.g., physiology, reproduction) and indirectly (i.e., ecological interactions). Direct effects of temperature can be conceptualized in thermal (or temperature) performance curves (TPCs) [12]. TPCs for important biological traits, including metabolism, reproduction, or feeding rate, generally exhibit left-skewed, unimodal shapes across a range of temperatures (Figure 1; [13]). The performance of a given trait generally increases gradually from a critical minimum temperature (CT\text{min}) before reaching a maximum at an optimal temperature (CT\text{opt}) and then decreases rapidly to a critical maximum temperature (CT\text{max}). Using this model, it becomes apparent that small changes in temperature can have direct effects on organismal performance that can affect their physiology, behavior, and population size [14]. Further, changes that affect one organism may have indirect effects on other organisms by altering their interactions. For example, warming may elevate a predator’s metabolism, which would require it to eat more prey to meet nutritional demands [15]. In this case, predators can mediate an indirect effect of warming on prey populations.

The nonlinear nature of a TPC also gives insight as to why nighttime and daytime warming may generate different effects on an organism and its interactions within a community [16,17]. When experiencing an environment near T\text{min}, an increase in temperature will have a relatively small, positive effect on trait performance (Figure 1, blue arrow). In contrast, for an organism experiencing an environment near T\text{opt}, the same increase in temperature will produce a large, negative effect on trait performance (Figure 1, red arrow). While there are exceptions, nighttime is generally cooler than daytime; therefore, the effects of warming at night may be akin to the left side of the TPC and the effects of warming during the day akin to the right side of the TPC. The importance of this distinction was recently demonstrated using a system of spider predators, grasshopper herbivores, and plants at the Yale-Myers Research Forest [18]. In that system, daytime warming caused thermally stressful environments for predatory spiders. To avoid heat stress, the spiders moved down towards the ground where it was cooler and became inactive. In response to reduced predator activity, grasshoppers spent more time feeding, and their herbivory suppressed the biomass of plants. In contrast, nighttime warming allowed the spiders to become more active, which reduced grasshopper activity and increased plant biomass. Thus, BT Barton and OJ Schmitz [18] demonstrated that daytime warming experiments may produce misleading conclusions about the effects of climate change that is dominated by nighttime warming.

The timing of warming may be important for additional reasons not conceptualized in TPCs. Daytime and nighttime differ in many ways besides temperature, including humidity and light levels. Indeed, recent work has shown that the net effect of nighttime warming on food web interactions can be light dependent [19]. While not well-studied in the context of daytime versus nighttime warming, evidence suggests that the net effects of warming are affected by other abiotic factors [20]. Further, plant and animal physiology and behavior may be constrained by photoperiodism and/or circadian rhythm such that certain activities occur regardless of temperature. As such, organisms may be unable to take advantage of periods of time that are thermally optimal if their biological rhythms limit activity [21].

**Figure 1.** Thermal performance curve (TPC) depicting how temperature influences performance of a given trait. CT\text{min} and CT\text{max} are the minimum and maximum temperature that an organism can perform at for a given trait, and for many traits (e.g., respiration rate) temperatures above or below these values are lethal. T\text{opt} is the optimal temperature for that trait. Because of the uni-modal and asymmetrical shape of most TPCs, warming may affect trait performance differently depending on whether there is an increase in daytime (T\text{day} + X; red arrow) or nighttime temperature (T\text{night} + X; blue arrow).
Unfortunately, field studies examining food web responses to warming rarely enlist nighttime warming treatments, and fewer still have compared daytime and nighttime warming to determine if their effects are comparable. Most field studies manipulate daytime temperature because it is logistically easier to manipulate solar energy to create different warming treatments [22]. One of the most popular methods has been open-top chambers (OTCs; [23-26]), which create a greenhouse effect that warms the contents. However, since solar energy is only available during the daytime, OTCs mainly warm when the sun is visible, with a smaller degree of warming maintained throughout the night (Figure 2 and Figure 3). This is concerning for at least two reasons. First, since nighttime-dominated warming is common, many—if not most—climate warming studies disproportionately warm during the day and therefore fail to test realistic predictions. Second, while models such as TPCs suggest that daytime and nighttime warming may have different effects, there are few empirical studies to evaluate those differences (but see [18]). Thus, it is unclear how many warming experiments contribute to our understanding of the effects of actual climate warming, and how many provide misleading conclusions.

To encourage ecologists to conduct experiments that include nighttime warming treatments, we offer a review of methods to manipulate nighttime temperatures in terrestrial environments. Some of these methods are obvious and already used by ecologists, while others are effective but difficult to implement. Therefore, for each of the methods presented below we discuss the method setup, feasibility, pros, cons, and relative cost (Table 1). Our hope is to provide future investigators with a reference and inspiration to expand their methodological repertoire. We also hope to encourage our colleagues to think “outside-the-box” and find unique solutions so that we can test these important predictions about the effects of global climate change on earth’s biota.

### NIGHTTIME-WARMING METHODS

#### Energy Source: Electricity

**Electric Heaters:** Electric heaters are an effective way to increase ambient temperatures [18,27-29]. The magnitude of warming provided by an electric heater will depend on experimental scale, number of heaters per site, and the angle placement of each heater [27,30]. This heating method is adaptable to different kinds of field experiments, including mesocosms [18,31] and large open plots [27,32].

Different types of electric heaters include convection and infrared (radiant) heaters. Convection heaters warm air, which then rises and circulates in an enclosed area. As a consequence, convection heaters tend to warm large areas unevenly and are inefficient because the heat escapes upward and away from the experiment [33]. In contrast, infrared heaters warm objects instead of air, which provides a more instantaneous heating effect compared to convection heaters. Infrared heaters are most common in ecological field experiments, and we were unable to find
Electric heaters have many benefits for warming experiments. First, electric heaters can be controlled with precision by using a combination of timers and thermostats. Timers can maintain daytime and nighttime warming treatments by turning heaters on or off during a predetermined period of time. Within that period of time, temperatures can be regulated with electronic thermostats that turn heaters on or off when temperatures maintain precise levels of warming relative to unwarmed controls. Second, heaters are available in a wide range of powers (measured in watts), allowing a researcher to tailor the warming effect to their specific experiment. Third, heaters can be used individually or in groups of multiple heaters to create warming treatments in different sized mesocosms or plots. For example, four heaters (250 W Exo Terra Mansfield, MA, USA) created 4°C nighttime warming in a 3.2 m² x 1.8 m mesh enclosure (Lumite, Alto, GA; Figure 4), while one of these heaters in a smaller mesh enclosure (1.0 m² x 1.2 m) created similar nighttime warming (Figure 5). Finally, electric heaters are commercially available and relatively affordable. Many options are readily available online or at common stores, including heaters that are marketed for the reptile and amphibian pet trade. A single electric heater can be purchased for as little as $50 USD (250-watt Exo Terra Ceramic Heater and lamp fixture), although prices can increase substantially with other systems. Additional features such as timers and controllers cost approximately $75 USD (Emerson 16E09-101 Electronic Temperature Control and Woods 5011WD Outdoor 24-Hour Plug-In Mechanical Timer) and are also readily available for purchase.

While the electric heater itself may be inexpensive, a significant limitation of this approach is that infrastructure to provide electricity in the field can be difficult to obtain and expensive to install. Possible sources of electricity include field stations or plots near buildings. Additional options for field electricity are generators, batteries, or solar panels. Generators have the disadvantage of simultaneously creating exhaust fumes [34] and noise pollution [35] which could impact ecological communities [36]. Batteries would require frequent recharging or replacing. While solar panels could be used to charge batteries in situ, the process of converting solar radiation into electricity, then converting the electricity back into heat is extremely inefficient and makes implementation in field experiments economically prohibitive (Goal Zero, Personal Communication, June 16, 2017).
that last longer may still reliably produce an increase in average temperature. For example, a used Orchard-Rite Chevrolet 454 Wind Machine can cost $25,000 USD. While the size and costs of wind machines may make them impractical to implement in large-scale studies, we encourage researchers to consider adapting the general principle into smaller experimental scales. For example, vertical gradients of temperature exist within plant canopies and it may be possible for scientists to capitalize on these gradients with battery-powered fans at small scales. However, we are unaware of data to evaluate the effectiveness of such a method.

Energy Source: Combustion and Other Chemical Reactions

Fire: Heaters, torches, or pots filled with lit fuel were once a common method used to keep orchard crops from freezing [45]. Originally, these heaters would have to be individually lit and maintained each night, creating higher operating costs for it than other vineyard frost protection methods (e.g., wind machines and sprinkling) [45]. However, modern updates to this method include centralized fuel systems which greatly reduced labor [46]. Some pots, also known as smudges, were once used to create black smoke at dawn in an attempt to reduce the amount of solar radiation reaching the fruit [47]. This method was believed to slowly thaw fruits that were frozen overnight. Overall, orchard heaters and smudge pots are less
common today due to rising oil prices and restrictions in many areas to decrease air pollution [38].

An obvious benefit of this approach is that it does not need electricity. Additionally, this method has a low cost. The price for producing these heaters with 55-gallon drums would be approximately $110 USD in addition to the price of fuel. However, this warming method would require an increase in labor and potentially alter the study system’s abiotic environment by producing smoke. Air pollution (smoke) from fire could alter chemical cues by elevating carbon dioxide and other chemicals levels [48] with diverse effects on animals, plants, and their interactions [49,50]. One way to implement this method in field experiments would be using a 55-gallon drum filled with fuel and ignited to burn throughout the night (Figure 6). Commercially available “patio heaters” that are fueled by propane canisters may provide a modern alternative to fuel-filled drums. However, while these methods could work for extremely large mesocosms or field experiments, the imprecision, logistical challenges, and risks of fire may make this impractical for many studies, especially those in the laboratory.

**Hand Warmers:** Commercially available hand warmers are potential sources of heat for warming experiments. These small, self-contained heaters can be placed within experimental units to increase temperature. Several different types of hand warmers are available. Among the most readily available hand warmers are non-reusable air-activated hand warmers sold by companies such as Hot Hands or Grabber. These hand warmers create heat using an exothermic reaction (oxidation of iron) and can increase nighttime temperatures relative to control treatments (Figure 7). Other options include reusable hand warmers powered by the combustion of butane, as well as rechargeable electric versions.

Hand warmers have been used previously in field experiments. One study has successfully used hand warmers to create a soil temperature gradient of approximately 20°C [51], while another study used hand warmers in conjunction with insulating tree wraps to increase tree trunk temperatures by 7°C [52]. Using a more powerful version of this technology designed for warming the contents of shipped boxes (UniHeat Packs, Chromsack Ventures, Montana, USA; Mycoal warmpacks, Northbrook Industrial Estate, Southampton, UK), previous studies have increased temperatures within bird nest boxes by several degrees during both the daytime and nighttime [53,54].

This method requires no electricity and is fairly inexpensive. The price for 40 pairs of non-reusable hand warmers is approximately $28 (HotHands Hand Warmers), approximately $12 for a single butane hand warmer (6-hour Zippo Hand Warmer), and approximately $20 for a single rechargeable hand warmer (5200 mAh Cypers Double-Sided Rechargeable Hand Warmer). However, depending on the scale of the experiment and number of replications, this method could quickly become a less cost-effective option. For example, even in small enclosures we observed less than 1°C warming, even with eight hand warmers (Figure 7). While reusable battery-operated hand warmers are unlikely to produce byproducts that influence an experiment, air-activated and butane-fueled hand warmers could create unwanted chemical alterations in the environment through the release of chemical
Another concern is that the curtains are a physical barrier that could deter the movement of organisms, including nocturnal pollinators [58], into and out of the plot. Finally, reflective curtains could unintentionally impact other abiotic factors such as raising humidity levels or changing local wind and precipitation patterns [57].

**Radiant Objects**

Besides the earth, any object may potentially store solar energy during the day that can be radiated at night. Miller et al. [16] recently used this process to create nighttime warming treatments in a manipulative field experiment. Their method was to fill black plastic bags with water, which were placed next to plots [57]. Another concern is that the curtains are a physical barrier that could deter the movement of organisms, including nocturnal pollinators [58], into and out of the plot. Finally, reflective curtains could unintentionally impact other abiotic factors such as raising humidity levels or changing local wind and precipitation patterns [57].

**Energy Source: Solar Radiation**

**Reflective Curtains**: Reflective curtains reflect infrared radiation leaving the ground much like “cloud greenhouse forcing,” which is when clouds absorb heat emitted from the surface and reemit the heat back to earth [56]. These setups are usually designed so that an electric motor extends a reflective curtain over an experimental plot at dusk (see C Beier, B Emmett [57]). By covering the plot at night, the curtains prevent heat radiating from the earth to escape into the atmosphere, thus creating nighttime warming treatments. The curtains can be retracted during the day, so that ambient temperature and other abiotic factors are similar between control and warmed treatments. Price for reflective curtains will vary based on the material used to construct the curtain and any added automation [22].

Although effective, reflective curtains have several important limitations. Control plots with no reflective curtains could experience similar changes in temperatures to warmed plots if there is cloudy weather [57]. Similar to reflective curtains, clouds can trap radiation leaving the ground at night and radiate it back down to the surface [5]. With this method, nighttime warming treatments can have lasting effects on daytime temperatures. For example, soil temperatures during the day of a nighttime warming plot were 1°C higher than control plots [57]. Another concern is that the curtains are a physical barrier that could deter the movement of organisms, including nocturnal pollinators [58], into and out of the plot. Finally, reflective curtains could unintentionally impact other abiotic factors such as raising humidity levels or changing local wind and precipitation patterns [57].
temperature decreases. For example, the effectiveness of the approach will be impacted by sun exposure, which can vary with tree and cloud cover, as well as latitude [22]. Another potential issue is that natural weather events (e.g., high winds or thunderstorms) or animals could damage the water bags. Additionally, this method may require insulation at night to maximize the warming effect, which is logistically demanding. For example, Miller et al. covered enclosures with plastic bags each night and returned to uncover them each morning. Covering enclosures with plastic bags may alter other aspects of the environment (e.g., wind, humidity, light), but confounding effects may be eliminated if both treatments are covered (i.e., control enclosures and warmed enclosures with water bags). Finally, this method may also increase daytime temperatures, reducing its utility for studies that aim to compare daytime and nighttime warming (Figure 8) [19].

Additional Methods

Spatial Variation: Conducting experiments at multiple locations that differ in temperature is another way to test hypotheses about different types of warming. This spatial variation method is common in ecological experiments for comparing differences in organismal response to some factor along a natural environmental gradient in lieu of a long-term experiment [59]. Applying this method to compare the effects of nighttime warming would require at least two sites that are ecologically similar and experience the same daytime temperatures, but have different nighttime temperatures [6,7].

One potential benefit of the spatial variation method is that it may be relatively inexpensive, but this would depend on factors such as travel costs. Additionally, this method would require no electricity. However, finding sites with specific types of warming could be challenging. If these sites differ in ways other than temperature, the interpretation of results may be confounded by other factors (e.g., soil type, moisture, species present, etc.).

Temporal Variation: Temporal variation in nighttime temperatures could be used to create nighttime warming treatments. Broadly, this method would work by conducting the same experiment at various times throughout the year when nighttime temperatures were different. During each experiment, daytime temperature would be standardized (or statistically accounted for) and nighttime temperatures would be unaltered from natural conditions.

An advantage of this method is that there would be no change in study site between treatments (in contrast to the spatial variation approach), which minimizes site effects. However, phenological changes within a site could alter the composition of the community and must be considered. Similarly, many abiotic factors other than temperature vary during the year, including precipitation and carbon dioxide concentration [60].

CONCLUSIONS AND OUTLOOK

Creating nighttime warming treatments for field experiments is not impossible but may require creativity. The value of the methods listed here are likely to vary considerably as a function of the resources available to an investigator (e.g., electricity, funding), scale of the study (e.g., duration of experiment, size of the experimental unit), and a host of other factors. Our review is a resource, but one that must be adapted to specific study systems and questions. Ecological interactions are generally very context dependent [61], so it should be expected that studies could produce inaccurate conclusions about the effects of climate change if experimental treatments differ from actual climate warming [62]. Thus, we encourage ecologists interested in understanding the effects of climate change to put forth the extra effort to ensure that their experiments are using appropriate treatments and testing appropriate predictions.

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