

PERSPECTIVES

Weather and insects in a changing climate

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INTRODUCTION

The humourist Mark Twain is quoted as saying, “Everyone complains about the weather, but no one does anything about it.”² A century later, we realize we have been doing something about it all along. But unlike the intent of the joke, human effects on weather and climate will have dire consequences for the future of many biological systems. The drivers of this change are socio-economic, but the consequences – and our capacity to anticipate and mitigate them – require insight from ecology.

The effects of weather on humans’ vital biological processes are obvious only in the extreme. Our physiologies maintain steady thermal states and we have extended our habitable range to adverse environments with clothing, shelter, and fire. However, the development of modern ecology in the first decades of the 20th century gave entomologists an appreciation of the pervasive role of weather on insects and the ecosystems they inhabit. Insects soon served as models of the ecological relationships between climate and life systems, because of the observable effects of weather on the behavior, development, and survival of insects (Uvarov 1931). The small size, diverse and abundant populations, and economic importance of insects has made entomology a major contributor to theories and methods that are relevant to understanding ecological systems.

This essay explores the ecological relationships between insect populations and climate and weather, which are aptly distinguished by Mark Twain as “climate is what we expect, weather is what we get.” The subject is too large to review critically in this forum; instead, I illustrate an approach that I believe provides useful, general insights to the possible ecological consequences of climate change, based mostly on my experience in forest entomology.

Insect outbreaks can propel major ecological disturbance in forests by affecting forest composition, productivity, and structure. Forest ecosystems, in turn, play a critical role in the terrestrial carbon budget and so have the potential to mitigate the effects of climate change, if healthy, or exacerbate them, if not. Compared to long-lived trees, which modulate the relatively slow transitions that are characteristic of forest ecosystems, insect populations change rapidly – in part because their dynamics are more immediately responsive to ambient weather than are the trees they inhabit. Insects are also highly mobile and can move to more favourable areas as climate-related shifts in conditions occur. Their fast-moving outbreak dynamics are indicators of emerging and future changes in forest disturbance patterns.

Some of these changes are already underway. Our focus on insects as disturbances to forests has resulted in detailed scientific knowledge of their bionomics and in compilations of essential survey records. Forest entomologists

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²The origin of the remark is attributed to Twain’s friend, Charles Warner

make significant contributions to field methods in ecology and analytical tools that advance our understanding of quantitative ecology, population dynamics, and systems analysis. Weather and climate affect ecological relationships at each of these levels of inquiry.

MODELS FOR INFERENCE

Models to analyze the relationships between insects and climate may be empirical or process models. Empirical models focus on statistical relationships between, for example, observed patterns of insect damage and meteorological variables. The structure of these models is not necessarily causative but describes correlated events. In bioclimatic studies, empirical models are sometimes called envelope or niche models, following early definitions of the niche as locations where environmental conditions permit an organism to live – that is, its habitat.

By comparison, process models characterize functional variation in key ecological relationships. These models reflect the contemporary view of the niche as the ensemble of traits that determine survival and reproductive success of an organism in particular environments – that is, its fitness (Chaine 2010).

Habitat models serve as the starting point of most quantitative investigations in population ecology to test hypotheses and estimate model parameters. These models draw their evidence primarily from historical surveys of insect distributions or their impacts, and weather. Their value is a function of the extent, continuity, and accuracy of the data used. Canada is fortunate, because records exist of annual overview and point surveys of insects and diseases compiled by the Forest Insect and Disease Survey of the Canadian Forest Service between 1936 and 1996. These data provide baseline descriptions of where species have been found and outbreaks observed.

Invasion and conservation ecologists, often confronted with little data on the life histories of introduced or rare species, can make good use of habitat models for initial estimates of climate suitability and relative risk. For example, plant-hardiness zones are habitat models based on observed co-occurrence of plant assemblages (McKenney *et al.* 2007). Overlay of plant-hardiness zones on survey records of invasions of winter moth, *Operopthera brumata* L., and balsam wooly adelgid, *Adelges piceae* Ratzeburg, indicate boundaries in the frequency of occurrence of these two species that are congruent with different plant-hardiness zones. These results suggest that historic climatic gradients have, to date, stalled further spread of these species in Atlantic Canada (Nealis *et al.* 2016; Quiring *et al.* 2008). However, climate change will shift the zones' boundaries and possibly the area susceptible to accelerated invasion.

Where survey data are sufficiently rich, habitat models can reveal key processes that characterize population dynamics of insects, especially where apparent thresholds or steep environmental gradients correlate with the relative abundance of an insect. Historical survey data from British Columbia (BC) show relatively infrequent outbreaks of the mountain pine beetle, *Dendroctonus ponderosae* (Hopk.), outside the -40° C minimum winter isotherm, thereby identifying vulnerability of the beetle's overwintering life stages to low temperatures. This simple map accounted for previous incursions of mountain pine beetle into high-elevation forests during warmer winters (Logan and Powell

2001) and recent range expansion into new host forests made susceptible by warmer conditions (Safranyik *et al.* 2010).

Such direct and consequential effects of weather on insect populations, however, are less common than indirect effects, which ripple through trophic and physical interactions alongside other weather-dependent factors important to an insect's life. This higher-order complexity can yield problematic results for habitat models. For example, there are so many possible meteorological variables and indices to test that significant but spurious associations become probable and inferences misleading. A related problem is significant interactions that defy biological interpretation. Unless there is prior knowledge of system structure, there are few criteria to determine which variables to include in a model. These are pertinent limitations in projecting future states under climate change based on historical correlations.

Process models focus on functional ecological relationships to improve inferences regarding fitness under different environmental conditions. Fitness is an attribute of individuals in nature. Process models can take advantage of modern computing power to calculate the individual fitness of thousands of members of a population that may vary slightly in their intrinsic responses to weather variables. This enables realistic simulation of *per capita* reproductive success and prediction of inter-generation rates of change in population density under variable conditions (Régnière *et al.* 2012a).

In practice, empirical and process approaches to modelling ecological relationships between weather and insects are complementary. Their successful application often depends on practical limits of available information and model objectives. However, ecological questions increasingly require dynamic models to accommodate changing conditions in the fundamental processes underlying the survival and fitness of organisms. There are few factors more fundamental to terrestrial ecological systems than weather and we know it is changing. It is no longer sufficient to predict future behaviour of forest ecosystems simply by analyzing historical patterns of outbreaks and disturbance. We must aim for the deeper inferences that come from analysis of the ecological processes that determine the distribution and abundance of organisms today so those same models can project the future.

PHENOLOGY MODELS

Phenology models reproduce the observed seasonal occurrence of critical events in an insect's life history. They are central to the analysis of ecological relationships between weather and insects. At their simplest, phenology models describe the empirical relationships between particular weather variables and seasonal events, such as temperature and the timing of an insect's emergence from hibernation in a particular habitat. The eco-physiological relationships included in phenology models reflect intrinsic, evolved characters that are not likely to change as fast as ecological conditions. When we scale the entire life history of an insect and the ecological events that determine its fitness via a phenology model, the model becomes a tool to probe the species' specific seasonal experience and the ecological processes that determine its fitness in any location and time.

Temperature is the weather variable with the most profound eco-physiological effect on insects. There are also many practical reasons to use temperature as the driving variable in phenology models. Temperature is the easiest and most commonly measured meteorological variable. Historic normal and real-time records are available for thousands of fixed points, and realistic interpolations can be calculated using environmental gradients known to affect temperature – for example, elevation – to construct climate surfaces. Temperature fluctuates periodically within normal limits on diurnal, seasonal, and annual scales, in patterns associated with explicit, fixed geo-references. Day-to-day temperatures are autocorrelated, allowing realistic, short-term daily temperature records to be simulated from climatic normals. Although other meteorological variables such as precipitation may also be important to an organism's fitness, fluctuations in air temperature are fluctuations in thermal energy that drive variation in most other micro-scale factors in an insect's environment. Gradients in thermal energy also account for regional-scale variation in atmospheric pressure and consequently most large-scale weather patterns. Given these correlations between temperature and weather conditions, adding meteorological covariates may confer marginal additional benefits for the practical objective of scaling eco-physiological events within the realistic limits of predicting future weather.

Statistical models of the relationship between the rates of insect development and ambient temperature transform insect time to a temperature-dependent scale. Originally, these models were derived from field observations of the duration of life stages at ambient temperature. The best-performing phenology models today use estimates of rates of growth and development under controlled, laboratory conditions with sufficient sample sizes to capture individual variability. The added advantage of laboratory estimates is they are independent of observed, seasonal events in both the weather and the insect population: they measure the process directly. This means empirical field data can be used to test and calibrate working phenology models. Degree-day models are the simplest models to fit such data and have wide applicability in entomology (Gilbert and Raworth 1996). However, the availability of more detailed experimental data and computational tools to fit flexible, non-linear functions enables simulation of variable, stage-specific development rates over the full range of seasonal temperatures experienced by insects in nature (Régnière *et al.* 2012a).

Modelling phenology over an entire year rather than just over the insect's active season allows simulation of a sequence of consecutive 'generations', which translates the cumulative effects of variable weather to a measure of climatic suitability based on fitness. For example, the ability to reproduce the phenology of a complete generation of gypsy moth, *Lymantria dispar* L. – including its oviposition, diapause and active development periods – made it possible to evaluate the probability of its survival over consecutive generations – and therefore its relative invasion risk – in present and future environments (Régnière *et al.* 2009). There are also immediate, practical applications. The gypsy moth phenology model supports a decision-support protocol enabling more efficient deployment of traps for detection, evaluation of probable persistence of founder populations, and optimal timing of pesticide applications for eradication (Nealis 2009).

These applications illustrate how phenology models' can be used to provide a relevant scale to examine other ecological processes in their appropriate spatial and temporal contexts and to go beyond simple correlations between weather and observed fluctuations in insect populations.

A CASE STUDY: SPRUCE BUDWORMS

Spruce budworms (*Choristoneura*) are among the most well-known forest insects in Canada. Many significant advances in forest entomology owe their development to spruce budworm research, including life tables, simulation and mathematical models in population dynamics, and systems analysis in resource management.

The influence of weather always figures in research on spruce budworm ecology, but how weather influences fitness is only partially known, and the evidence is difficult to apply to practical questions. Isolated weather events such as killing frosts or the migration of moths on storm fronts may contribute to survival of insect generations and egg recruitment, but the effects are variable and often compensatory over the life cycle. More to the point, notable meteorological events are not especially predictable and often affect populations only temporarily or locally. Entomologists need models that wed normal weather to seasonal events for several generations of an insect's life history if they want to understand general ecological processes that determine change over areas where species persist now and may or may not persist in the future.

Wellington *et al.* (1950) first noted spruce budworm outbreaks were preceded by years of warm, dry weather in the month of June. This was a habitat-based inference. It could identify the times and places affected by weather but not how or why this occurs. June is the main feeding period for budworms, and behavioural studies had shown the caterpillars feed more continuously and develop faster in dry, warm conditions – conceivably conferring survival benefits. In addition, warm, dry summers promote production of pollen cones in mature conifers, an early-season resource for small budworms that also provides a beneficial “greenhouse” effect in cool northern environments (Wellington 1950). Both weather-related factors hinted at the importance of seasonal timing, but despite concerted research, their net effect on fitness remained unclear (Greenbank 1956).

In terms of population analysis, the problem stemmed partly from difficulties in sampling early-stage budworms (Fig. 1). Eggs, overwintering, and spring-foraging budworms each occupy different parts of the sample universe and are either cryptic or in motion, so between-stage rates of survival are difficult to estimate. Consequently, the focus of quantitative analyses shifted to survival of large, feeding larvae for which sufficient population density estimates were available. The analyses showed that during the feeding and subsequent pupal stages, natural enemies – not weather – had a greater effect on survival and, as a result, spruce budworm population dynamics came to be viewed as a predator–prey relationship, with weather a stochastic effect imposing variation but not trend (Royama 1984). However, during the early stages of the budworm's life history, the insect neither feeds nor is greatly affected by natural enemies, leaving weather the likely dominant driver of environmental variation in their survival. By relegating the role of weather to ‘noise’ in the analysis of population

dynamics, spruce budworm studies of this time essentially dismissed survival of small budworm larvae from analysis of generation survival.

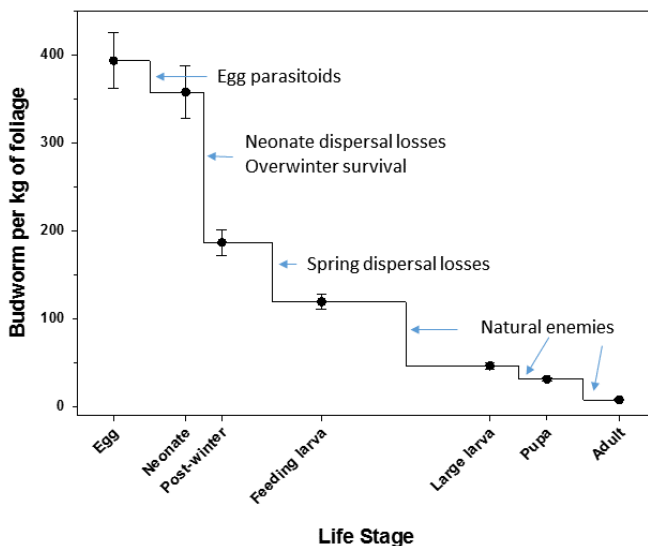


Figure 1. Within-generation changes in western spruce budworm per kilogram of foliage with key factors affecting stage-specific survival. Means (SE) calculated from annual census data from several outbreak populations in the southern interior of British Columbia, 1997–2015.

Yet, for budworms, a great deal goes on in these early stages, and weather conditions run the gamut of annual extremes. Eggs hatch in summer, and neonates disperse immediately away from their egg mass in search of hibernation sites. Larvae must then survive a long dormant/diapause period, first in warm summer conditions, then months of minimum northern temperatures, then variable spring conditions. The budworms do not feed during these early stages and must endure this prolonged period solely on nutrition provided in the egg. Perhaps because of dwindling energy reserves, they emerge in spring well in advance of fresh buds and forage throughout the forest canopy for sustenance. It is not surprising that variation in field estimates of survival, derived after these various processes have taken their toll, has bewildered the search for patterns of survival.

I began to unpack the black box on survival of early-stage budworm when I observed how critical early-season pollen cones were to the survival of jack pine budworms, *C. pinus pinus* Free. All conifer-feeding budworms emerge from their overwintering hibernacula well before current-year buds are available to them. Their spring dispersal through the forest canopy in search of the earliest buds can result in significant losses to populations (Nealis 2016). Nonetheless, field observations of western spruce budworm, *C. occidentalis* Free., estimated the optimal ‘head-start’ for emerging budworms was more than two weeks before 50% of new buds were available (Thomson *et al.* 1984). Insight into this counter-intuitive adaptive syndrome meant going back to the beginning of the insect’s

life cycle and measuring changes in fitness as life stages passed through seasonal pressure points. As these processes were evaluated, the phenology model was enriched iteratively until it reproduced measured population densities, then observed historical outbreak patterns, and – finally – the likely future of forest disturbance under climate change.

In our calendar time, the nine-month period from oviposition to spring emergence constitutes three-quarters of budworms' annual life, during which considerable weather-related mortality occurs (Fig. 1). Eggs are laid in mid- to late-summer and, unless exposed to significant frost conditions, the effects of weather at this stage appear to be inconsequential. The probability of killing frosts for budworms depends on where and when eggs are laid. This is determined by the seasonal period of moth dispersal and oviposition, which are governed by the temperature-dependent pace of feeding and maturation earlier in the season – that is, the timing of oviposition is determined entirely by temperature. To test this, we simulated seasonal development with local temperatures in a phenology model. The results demonstrated that the calendar period of adult activity can be predicted and compared with historical meteorological data to calculate the likelihood of killing frosts during the adult and egg stages at any location (Nealis and Régnière 2014). In budworms, this direct effect of cool, seasonal weather on development time and subsequent likelihood of exposure of adults and eggs to killing frosts sets explicit northern and elevational limits on climatic suitability (Régnière *et al.* 2012b; Régnière and Nealis 2019a).

After eggs hatch, larvae disperse to hibernation sites and prepare for winter. Once the larvae are sheltered in their hibernacula, cool weather favours their survival, whereas warm weather during this period demands energy and drains the fixed energy reserves available to dormant larvae. As during the egg stage, the weather conditions encountered by these dormant larvae are related to previous, local phenology. In warmer locations where oviposition occurs earlier in the season, progeny often must endure a longer period of heat stress, with negative consequences for survival. Already in this earliest period of budworm development, weather exerts a “pinching” effect on the primary environmental range of budworm. In cool northern and high-elevation forests, delayed maturation and oviposition exposes moths and eggs to killing frost, whereas in warmer latitudes and at lower elevations, early oviposition results in budworms consuming energy reserves required to survive winter.

Winter weather appears relatively benign to budworms over much of their range. The crucial events occur later, after physiological diapause is complete in late winter but before the weather warms up enough for dormant budworms to emerge. It is during this transition period that the cumulative effects of energy consumption begun during the warm days of the previous season take their toll: budworms with insufficient energy reserves to endure the final three months of dormancy perish. Warm weather during this late-winter period exacerbates stress and further increases mortality. It is not cold winters but warm temperatures during transition seasons that determine local fitness of small budworm larvae between hatching and emergence nine months later (Nealis and Régnière 2016).

The precocious spring emergence of budworms weeks before budburst suggests an urgency to secure a feeding site. This hypothesis prompted Thomson

and Benton (2007) to develop a habitat-based model that proposed an observed change in outbreak history of the western spruce budworm on Vancouver Island during the 20th century was related to local sea-level warming. The increase in temperature caused earlier emergence of budworms but apparently no change in the timing of bud flush. The inference was the resulting greater asynchrony increased mortality of foraging budworms and reduced the likelihood of outbreaks. However, simulations using our fitness-based phenology model, corroborated by direct field measures of budworm survival during the foraging period, show budworm synchrony with the host during this stage is a very robust process. Budworms can survive several weeks of foraging in the spring before bud-flush. The presence of pollen cones helps bridge this gap, and old needles also provide sustenance. Field studies showed that losses during this dispersal period do influence dynamics in important ways, but the losses are associated with previous defoliation and stand characteristics, not with weather-mediated synchrony of emergence and bud-flush (Nealis and Régnière 2009).

Spring emergence marks the beginning of the feeding period, with budworms and their food supply developing at their respective, temperature-dependent rates. A model predicting relative fitness of budworms as a function of normal, seasonal change in host-foliage quality examined how variation in this seasonal interaction affected inter-generation rates of change. Parameters were derived from field measures of emergence dates and contemporaneous suitability of developing foliage in the spring (Nealis and Nault 2005). The phenology model then tracked temperature-dependent rates of growth and development of feeding budworms and ultimate deterioration of foliage quality at the end of the growing season, also determined by independent field measurements. Together, these defined a phenological window for feeding and maturation, and resulting fitness (Nealis 2012). The result was a trade-off between time of spring emergence and subsequent time available for feeding before foliage became unpalatable. Early-emerging budworm gamble an early period of deprivation against the greater likelihood of maturing while foliage is most accessible. Consequently, the cost of early emergence may be offset by the benefits of improved survival and greater fecundity resulting from large feeding stages that coincide with succulent, rapidly growing foliage (Régnière and Nealis 2018). The phenology model allowed us to simulate the process under different seasonal conditions to understand the outcome for fitness across landscapes and through time.

The most recent fitness model includes all of these temperature-related effects on budworm across the range of its host (Régnière and Nealis 2019a). Spatial and temporal characteristics of seasonal temperatures appear to explain a great deal about the geographic range and population dynamics of western spruce budworm. At the most northerly latitudes and highest elevations, cool temperatures slow maturation of feeding budworms, decreasing their fitness through the effects of a rapid decline in host-plant quality at the end of the short season and exposing surviving moths and their eggs to killing frosts. At southern and lower elevations, warm weather exhausts energy reserves of dormant larvae, also reducing fitness. Between these limits, the model predicts climate suitability and identifies areas of optimal fitness. This is where increases in budworm populations are most likely.

The temporal view was equally interesting. Since 1950, climatic conditions in the BC Interior have improved the fitness of western spruce budworm steadily. The greatest increases have occurred since 2000, and match observed outbreak behaviour over the same period (Maclauchlan *et al.* 2018). It seems much of the historic, coarse-scale outbreak behaviour of western spruce budworm populations coincides with spatial and temporal weather effects on phenology which, in turn, influences fitness in the insect's annual acquisition of resources. When likely climate change scenarios are applied, they predict up-slope improvement in climate suitability for budworm survival will continue. Southern portions of the spruce budworm range in the USA will become too warm for dormant budworm, except at ever-higher elevations, with the insect eventually running out of host forests within climatically suitable territory. But in the north of the range, a greater area of climatic suitability will intersect susceptible host forests, and budworm disturbances will continue in northern and high-elevation forests and will also expand into forests where they have not occurred in historic times.

Just as an earlier, generalized phenology model of spruce budworm informed refinement of a fitness model for western spruce budworm, the western spruce budworm model provides inferences about spruce budworm.

One such inference concerns differences among host trees exploited by budworms in their respective forest eco-regions. The best place for any budworm to live is in a forest full of food where early- and late-season weather conditions are moderate, and where larvae emerge early in the race to find flushing buds without excessive risk. Getting there early is critical because the quality of host-foilage deteriorates quickly at the end of the season. In places and times where this phenological window favours feeding budworms, population increases are more likely.

Now consider the different host trees. Eruptive outbreaks of spruce budworms in the past century have been most damaging in fir-dominated forests – balsam fir, *Abies balsamea* (L.) Mill., east of the continental divide and other *Abies* species to the west. As a resource for budworms, the distinguishing characteristic of true firs over spruces (*Picea*), Douglas-fir (*Pseudotsuga*), and especially pines (*Pinus*) is that the old foliage of true firs remains relatively soft and palatable even at the end of the growing season. This makes the phenological window for true firs functionally wider than for other host trees, because budworms can continue to feed on fir later in the season and even back-feed on old foliage, causing even more damage. The result is that forests dominated by fir within regions of favourable weather support greater fitness of spruce budworms. In forestry terms, true firs are more vulnerable than other host conifers. This process-based assessment is consistent with empirical survey records, hazard ratings, and habitat models that associate the origin and intensity of spruce budworm outbreaks with particular forest types – now it has a fitness-based explanation.

To return to western spruce budworm in Canada, at present it is mostly associated with Douglas-fir, and tree mortality is relatively limited – again because of the budworm's difficulty in exploiting older foliage (Dodds *et al.* 1996). With climate suitability increasing at higher elevations in Canada, however, western spruce budworm may increasingly inhabit high-elevation

forests of subalpine fir (*A. lasiocarpa* (Hook. Nutt.). Disturbance patterns in those forests could change to resemble those of spruce budworm in the east (Nealis 2005).

A related question regarding disturbance patterns associated with climate change arises in eastern Canada, where climate suitability for spruce budworm also is improving northward (Régnière *et al.* 2012b) towards regions where spruce–fir forests are replaced by forests dominated by black spruce (*P. mariana* (Mill.) BSP). Black spruce is less susceptible to spruce budworm, because its buds typically flush later in the season than those of balsam fir and white spruce (*P. glauca* (Moench) Voss). Pureswaran *et al.* (2015) hypothesize that warmer conditions in the future will advance bud flush in black spruce, thereby increasing its susceptibility to spruce budworm. Although warmer weather may advance the calendar date of bud flush in trees, an increase in susceptibility of black spruce will occur only if warmer weather has no effect on the timing of decline in foliage quality the end of the season. In other words, if spruce budworm fitness is going to increase because of a climate-related change in black spruce phenology, it should result from a wider phenological window for foliage suitability, not simply from an advance in the season for existing, relative phenologies. A more likely change in the risk of significant budworm disturbance for northern black spruce forests is the incursion of more susceptible balsam fir and white spruce, whether this occurs as a result of management, climate change, or both. Resulting mixed-wood boreal forests would certainly increase the likelihood of significant damage to associated black spruce simply because of their proximity to highly susceptible balsam fir (Nealis and Régnière 2004).

WEATHER AND TROPHIC RELATIONSHIPS

Our ecological inferences agree with Wellington’s 1950 observation, noted above, that budworms flourish in forests of their preferred hosts during warm, dry Junes. It strengthens our knowledge and predictions about the geographic range of budworms, what constitutes a suitable climate where populations may increase to outbreak levels, interpretation of changing disturbance patterns, and the extent to which specific, key trophic relationships vary with weather. Despite this, however, the model provides only a proximate explanation of the mechanism. We know the phenological window is important, but the analogy eventually fails us because we still cannot see through that window to the ultimate cause. A more fundamental, fitness-based explanation is overdue.

Shortly after I published observations on the relationship between pollen cones and fitness of jack pine budworms (Nealis 2016), I received a letter from Prof. T.C.R. White in Australia, recently deceased. Tom “gently” (and gentlemanly) disagreed with my interpretation. Where I saw evidence of a delayed and reciprocal, density-dependent relationship between the host tree and the jack pine budworm, he saw further evidence that herbivores, including budworms, normally live in a ‘nutritional desert’. Their change in fortune, marked by outbreaks, is the result of environmental stress that accelerates senescence in the foliage of mature trees, releasing higher levels of soluble amino acids and thereby increasing food quality. White (1993) argued the presumption of a uniform source of adequate food for herbivores is untenable and contrary to the evidence from natural history. His alternative hypothesis of

outbreaks focusses on the fate of small, feeding larvae and their dependence on the availability of soluble amino acids. Availability peaks in perennial plants at the beginning of the growing season, when reserves stored in the roots are recruited to produce new foliage, and increases again at the end of the season, when nutrients synthesized by the foliage are shuttled back to storage in perennial structures. This is the reason why so many herbivores are either 'flush' or 'senescence' feeders. Stress, such as drought, increases plant quality for herbivores by further mobilizing amino acids. According to White, the greatest survival benefit of this change in nutritional quality accrues to small larvae as any improvements in their normally dismal survival rates increases fitness overall. In eruptive species such as spruce budworms, the positive effects on population growth will be most apparent in the years of transition from low to high densities when survival of early life stages increases (White 2018).

White's hypothesis implies an optimal feeding time with spatial and temporal variability in the adequacy of the resource, just as in our phenology model. Results of specific experiments that comprise that model are consistent with this idea. For example, repeated bioassays on both early- and late-stage budworm larvae on foliage at different stages of phenological development always show optima, indicating a seasonally dynamic condition in host-plant quality that is stage specific. The sharp decline in budworm fitness at the end of the season implies plant quality is a time-limited commodity. Regrettably, we have sparse quantitative population data on early-season nutrition and survival, particularly during the incipient stages of an outbreak. But what we infer from White's hypothesis is consistent with most of what we do know. Budworm outbreaks do tend to occur in drier parts of the budworms' ranges and are often preceded by notably dry, warm summers, especially in western populations (Maclauchlan *et al.* 2018). Defoliation is most intense in contiguous stands of over-mature trees that have copious, senescing foliage and a greater propensity to produce pollen cones. The greater fitness and higher density of budworm populations in these areas then actively export gravid moths, which homogenizes regional population densities and results in extensive and prolonged outbreaks (Régnière and Nealis 2019b).

The nutritional adequacy of the resource supporting these patterns varies in space and time. This can be generalized and incorporated with fitness-based models as seasonal processes scaled by temperature. If environmental stress does improve the nutritional quality of budworms' host trees, then climate change will have an additional effect on disturbance ecology beyond a geographic shift in climate suitability described above. Trees in all current forests survived because their genotypes were best suited to conditions prevailing during their growth under historic conditions. They will be stressed wherever climate change results in less favourable conditions. This could increase the area of susceptibility to outbreaks from small, scattered refuges envisaged by White (2018) to many areas where nutritional quality of trees has improved as a result of the stress of climate change. The result will be more frequent, explosive, and severe budworm outbreaks, as we now see in western Canada.

A premise of White's alternative hypothesis of budworm outbreaks is that changes in the survival of the small larvae associated with host quality yield commensurate changes in the density of subsequent generations. However,

improved survival early in budworm life history alone will not necessarily lead to greater generation survival, particularly where survival later in the life cycle is associated with density – whether dependent, compensatory, or circumstantial. Fitness models examine survival throughout the life cycle and at as many levels as possible to identify critical events affecting survival (Fig. 1). Nonetheless, White’s alternative hypothesis is eminently testable. The nutritional ecology of spruce budworms has been well studied, and nitrogen levels have been found to be most significant for budworm performance (Mattson *et al.* 1991). Efforts to identify other foliage-related indicators of budworm fitness have been equivocal but do provide methods that could be applied to estimating parameters that relate foliar nitrogen to phenology and stage of the outbreak cycle. These parameters would inform a new generation of process models that examine how seasonal fluctuations in foliage nutritional quality in different places and at different stages of an outbreak affect budworm fitness, as has been done for phenology at landscape scales (Régnière and Nealis 2019a). If White’s alternative hypothesis bears out, we will have a much more objective way to identify places, times, and tree species where the risk of spruce budworm outbreaks is changing.

EPILOGUE

The aphorism that opened this essay seems quaintly naïve today. However, Mark Twain was well-informed about the science of his day. The 19th-century scientific advances that he witnessed, and their application to industry and trade, enabled western countries to enter the 20th century at the peak of their economic power. At the time, some people believed even control of weather was only a clever invention away. In hindsight, these same scientific advances accelerated the climate crisis we face today. We are connected to Twain in history and its consequences.

It is these connections that ecology must decipher. I have always been interested in how weather and climate shape biological systems. I now realize, as many of us do, that climate change and future weather events will push and bend those systems in ways that are highly uncertain and will result in unwelcome surprises. Climate change is probably the gravest global ecological threat that humans have ever faced knowingly. Entomologists’ contributions to our understanding of climate–insects–forest systems may seem as small as insects themselves, but, in ecology, small things add up, and they never function in a vacuum. The emergent result of those many small, ecological interactions is what we seek to observe and model when we study insect populations and phenology to understand the future of ecosystem behaviour.

We may still be able to do little about the weather, but we can do more than just talk about it.

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