

Spatial patterns suggest movement of the filbert bud mite (*Phytoptus avellanae*) between plants and overwintering infestations in a hazelnut (*Corylus* spp.) orchard

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Abstract

Phytoptus avellanae is an eriophyid mite that feeds on and damages the vegetative and floral buds of hazel (*Corylus*) species by forming galls that impact hazelnut yield. *Phytoptus avellanae* has been identified on hybrid hazels (European hazel, *Corylus avellana* × American hazel, *Corylus americana*) that have been developed for hazelnut production in the eastern United States and Canada, but year-to-year variation in distribution and severity of *P. avellanae* damage within a field has not been studied. Additionally, whether *P. avellanae* differentially infests and damages the hybrid hazel plants vs. native *Corylus americana* plants is unknown. We assessed the spatial trends and species preferences of *P. avellanae* within a mixed-species field of hazels over a four-year period. All hazels were surveyed for galls caused by *P. avellanae* each spring and assigned a qualitative damage rating. We found that damage from *P. avellanae* was higher on hybrid hazel plants than on *C. americana* in each year of the study. In general, *P. avellanae* ratings increased towards the center of the field in most years. Our results showed that plants surrounded by infested neighbors often had higher damage ratings, suggesting that *P. avellanae* moves between adjacent plants. Understanding the within field distribution and host-plant preferences of *P. avellanae* will contribute to the development of scouting and management recommendations, provide insight on risk of mite movement between wild hazels and hybrid plantings in North America, and inform breeding efforts for this harmful pest.

Introduction

There are several pests of cultivated hazels (*Corylus* spp.) (Fagales: Betulaceae) worldwide (AliNiazee 1998). One of the most prominent is the filbert bud mite, *Phytoptus avellanae* (Nalepa) (Prostigmata: Eriophyidae) (synonymous with *Phytocoptella avellanae* Nalepa). This mite is a major pest of European hazel, *Corylus avellana* L., throughout Europe, Turkey, New Zealand, and the state of Oregon in the US (AliNiazee 1998; Denizhan et al. 2015). Mites infest floral and vegetative buds of hazels and feed on the epidermal cells, causing the buds to form galls and swell to several times their normal size (Castagnoli and Oldfield 1996). Ultimately, this “big bud” syndrome causes developmental failure and desiccation of the flowers (Castagnoli and Oldfield 1996). In Oregon, bud damage of up to 20% has been observed in susceptible cultivars of *C. avellana* such that development of cultivars resistant to *P. avellanae* is now part of the hazel breeding program at Oregon State University (Krantz 1974; Murray and Jepson 2018). As the global demand for hazelnuts is strong and growing, the US has established hybrid hazel breeding programs to expand the production of hazelnuts in the country using endemic hazel germplasm, including the American hazel (*Corylus americana* Walter) and beaked hazel (*Corylus cornuta* Marshall), crossed with *C. avellana* (Liang et al. 2012; Braun et al. 2019; FAO 2019). Since 2017, *P. avellanae* has been found at six experimental hybrid hazel (*C. avellana* × *C. americana*) plantings throughout Minnesota and Wisconsin, which is the first time it has been formally recorded for the Midwestern region of the US (Chediack et al. 2022).

Phytoptus avellanae was most likely introduced to North America via imports of cultivars of *C. avellana* derived from its native range in Europe (Lovett 1919; Ourecky and Slate 1969; AliNiazee 1998). The mite

species has since spread to hazels throughout North America, such as wild stands of the beaked hazel throughout the Pacific Northwest region where infestation levels of 20% or more of affected buds diminish nut yields (Brenner 1986). The arthropod has also been found in germplasm trials including the American hazel in the states of New Jersey, New York, Minnesota, Oregon, West Virginia, and Wisconsin and possibly Nebraska (ADF 2023; Oureky and Slate 1969; Thompson 1977; Burgess 1985; Brenner 1986; Molnar and Capik 2012; Cvrković et al. 2016; Hill 2020; Mehlenbacher and Molnar 2021; Chediack et al. 2022). Although *P. avellanae* has been previously studied on *C. americana* cultivars in hazelnut breeding trials, any preferences of the mite between the hybrid hazels (*C. avellana* × *C. americana*) and the American hazel, *C. americana*, have not been studied.

The life cycle of *P. avellanae* exhibits two different forms of varying complexity: gall and vagrant (Özman and Toros 1997a). Here we focus on the life cycle of the gall form, as described by Beber (1994) and Özman and Toros (1997b), because it is solely responsible for damage to the hazel buds. In spring, nymphs of *P. avellanae* migrate from last year's "big buds" to newly formed axillary buds (Fig. 1). The migration of nymphs takes place over a period of about 90 days starting in the spring when mean daily temperatures reach 9°C, with the most intensive migration taking place over an approximate two-week period therein (Burgess 1983; Webber et al. 2008; Fig. 1). Environmental and weather conditions are very influential on not only initiating the migration of the nymphs, but also the success of the migration, causing high mortality (Vidal-Barraquer et al. 1966; Jeppson et al. 1975; Beber 1994). For perspective, thousands of nymphs migrate from last year's big buds, yet only several reach and enter newly formed buds (Özman and Toros 1997a, c). Once inside new buds, nymphs settle on the meristematic apex and enter a resting period of approximately one month (Fig. 1). After the resting period, nymphs eclose to adults and begin reproducing, laying eggs on the meristematic apex of the buds or in the gap around it (Fig. 1). The formation of "big buds" can be observed as early as late summer when generations begin to overlap as eggs hatch and the infestation spreads to the outer scales of the buds (Fig. 1). The mites continue reproducing and feeding through the winter, cycling through several generations inside the buds, until the following spring where the adults of the last generation begin to lay eggs and produce nymphs that will migrate (Fig. 1).

While the life history, ecology and cultivar preferences of *P. avellanae* on *C. avellana* have been studied extensively in several regions (Krantz 1974; Thompson 1977; Burgess 1983; Burgess and Thompson 1985; Beber 1994; Özman and Toros 1997a, b, c; Webber et al. 2008), we are not aware of any studies that have documented the within-field spatial distributions of the pest, or how they might change from year to year. Documenting such patterns could provide insight into how this pest persists in or recolonizes fields. Eriophyid mites are thought to rely on wind for passive dispersal (e.g., between individual host plants or host patches), which could cause gradients in abundance or "hot-spots" across a field. Since eriophyid mites rarely destroy their host plants, long distance migration is thought to be seldom necessary for population survival (Lindquist and Oldfield 1996). However, eriophyid mites may also use larger, visiting arthropods of their host plants for phoretic dispersal (Keifer 1946; Sabelis and Bruin 1996).

The purpose of this study was to assess the spatial trends of *P. avellanae* infestation and hazel species preferences within a mixed-species hazel planting over a four-year period in the Upper Midwest region of the US, a novel geographic location for this mite species. We accomplished this by quantifying the level of *P. avellanae* damage to hybrid hazel and American hazel plants by recording whole-field data for 900 plants in a germplasm trial in northern Wisconsin. We hypothesized that we would see edge effects for annual recolonizations by windblown colonies, and perhaps random clusters or “hot-spots” if the hazel plants in the field had pre-existing mite infestations, or both phenomena. We expected infestation and damage of *P. avellanae* to be higher on American hazel plants rather than the hybrid plants because the American hazel is a naive host unlike the European hazel, which is a parent in the hybrid hazel genotypes in this study. To date, *P. avellanae* has only been found in wild stands of *C. americana* in northern Wisconsin in the Brule area (AC, personal observation). Except for this location, the mite is currently not known to exist in wild stands of American hazel (Ourecky and Slate 1969; Thompson 1977; Chen et al. 2007; JAF personal communication to HNS on 1 June 2020). Understanding distribution patterns can provide insight to underlying processes, such as *P. avellanae* dispersal, within field migration, and host preferences that can inform scouting and targeted control measures for the pest.

Methods

Field site and climatic data

The hazel planting used in this study is located in Bayfield, Wisconsin, US (46°50'19"N, 90°50'02"W) in a rural area comprised primarily of farmland interspersed with patches of deciduous forest (Fig. 2). This 1.21-hectare planting is a germplasm trial that contains 900 hazel plants: 368 *C. avellana* × *C. americana* hybrid seedlings (full-sib F1s), 256 individuals of *C. avellana* × *C. americana* clonal hybrids sourced from on-farm locations throughout the Midwestern US and Canada, and 276 *C. americana* wild-collected seedlings sourced from the Wisconsin Department of Natural Resources that were interplanted as checks for germplasm evaluation purposes and had not previously been screened for susceptibility to *P. avellanae* (Fig. 2). Plants were spaced 4.57 meters (15 ft) apart between rows and 1.83 meters (6 ft) apart within rows. All plants were planted between 2009–2012, making them between 4–7 years old at the start of our study in 2017. Plant survival was excellent with only one hybrid plant dying in 2020. Management practices consisted of an electric deer fence around the perimeter, an annual shielded application of Poast® herbicide (BASF Corporation Ag Products, NC, USA) to control grasses around the hazel plants and an annual spring fertilizer application of 33.6 kg/ha urea. Hazel plant genotypes that were characterized as top breeding selections were coppiced for propagation purposes over the years, including 29 hybrid plants between 2018 and 2019, and two hybrid plants in 2020. Coppiced plants were excluded from the study. Because the migration of nymphal *P. avellanae* is greatly influenced by climatic conditions, we collected climatic data including mean daily temperatures, precipitation, and windspeeds. Climatic data for each year of the study were collected from the National Weather Service's nearest weather station with sufficient historical data, located in Ashland, Wisconsin, 33 km away from the field

site (20.5 mi) (NOAA Station ID: USW00094929; Coordinates: 46° 32' 48.3354"N, -90° 55' 6.42"W) (Menne et al. 2012a, b).

Ratings

Each year during the last two weeks of May, all hazels were surveyed for galls caused by *P. avellanae* by inspecting the entirety of each plant. Individual hazels were assigned a qualitative *P. avellanae* damage rating of 0 through 4, with 0 representing 0% of the plant's buds galled, 1 representing 1–25%, 2 representing 26–50%, 3 representing 51–75%, and 4 representing 76–100% respectively. Ratings were made by the same observer each year from 2017–2020, with an additional observer taking ratings to provide a comparison in 2020. Galls were periodically collected, dissected, and confirmed to contain *P. avellanae* under a 45× magnification dissecting microscope each spring.

Data visualization and statistical analysis

All analyses and plots were conducted and created with R version 4.0.3 via RStudio version 1.4.1103 (R Core Team 2021; RStudio Team 2021). Heat maps were constructed each year to visualize the intensity and spatial pattern of ratings throughout the field (package, *code*: `ggplot2`, `ggplot` + `geom_tile`; Wickham 2016). In order to test for overall differences in mean temperature, total precipitation, and mean windspeed between years, we constructed linear mixed-effect models (LMM) with the year as a fixed effect and a term for month as a random effect (packages, *code*: `lme4` and `car`, *lmer* and *Anova*; Bates et al. 2015; Fox and Weisberg 2019). To test for differences in these climatic variables between months across years, climatic data for all four years was subset for each month and linear models were constructed with a term for year as a fixed effect (packages, *code*: `stats`, *lm*; R Core 2022). Finally, to test for differences in ratings across years, ratings were also analyzed as LMMs with a term for year as a fixed effect and a term for plant as a random effect to contend with any temporal autocorrelation from resampling of plants between years (packages, *code*: `lme4` and `car`, *lmer* and *Anova*; Bates et al. 2015; Fox and Weisberg 2019).

We built spatial models to examine how three types of predictors might explain within-field variation in damage caused by *P. avellanae*. Each year was analyzed separately. The first type of predictor was a term for hazel plant species (either *C. americana* or hybrid). The second was a spatial predictor to encompass localized trends or “hot-spots”. We did this by creating a “rook’s case” neighborhood structure (i.e., plants in the immediate adjacent places in the four cardinal directions as a variable that summed damage ratings for the four adjacent plants). We calculated rook contiguity-based spatial weights by creating a matrix of the ratings based on the field map for each year, filling lists with the matrices, converting the list to a raster (package, *code*: `purrr`, *map*; Henry et al. 2020), and then calculating the rating sum of the four neighbors, excluding missing plants (package, *code*: `raster`, *focal*; Hijmans 2023). The third type of predictors were field-scale spatial trends, including a unit northing (i.e., row within the field), a unit easting (i.e., column within the field), and their respective linear and quadratic and interaction terms.

All spatial autoregressive models were fit using damage ratings of *P. avellanae* as the response and the three types of variables as predictors (package, *code*: *spdep*, *errorsarlm*; Bivand and Wong 2018). We contended with potential spatial autocorrelation in the residuals by using a distance-based 3rd order neighborhood error structure in simultaneous autoregressive (SAR) spatial models; this structure generally included the nearest three plants in the surrounding two rows front to back and side to side and nearest two plants in diagonal directions (package, *code*: *spdep*, *dnearneigh*; Bivand and Wong 2018). To construct these neighborhoods, we identified neighbors of region points via Euclidean distance (in meters) within 2 m. We then calculated spatial weights for each year based on those distance-based neighborhoods using basic binary coding (package, *code*: *spdep*, *nb2listw*; Bivand and Wong 2018). Within each year, the significance of terms of interest in our models was explored using backwards selection methods and models were compared using Akaike information criteria (AIC). Residual plots were used to evaluate model assumptions of normalized errors and equal variance. We checked for evidence of remaining spatial autocorrelation in the residuals of best models using Moran's I test (package, *code*: *spdep*, *moran.test*; Bivand and Wong 2018).

Results

Climatic data

Mean daily temperatures ($\chi^2 = 24.18$, $df = 3$, $P < 0.0001$) and windspeeds ($\chi^2 = 19.75$, $df = 3$, $P = 0.0002$) differed between years of the study, but not annual precipitation ($\chi^2 = 2.22$, $df = 3$, $P = 0.5271$) (Fig. 3). Overall, 2019 had lower temperatures than 2017 and 2020, but 2020 had higher windspeeds than all other years of the study (Fig. 3). May, a critical month of *P. avellanae* migration from old galls to new auxiliary buds on plants, had the highest mean daily temperatures in 2018 compared to other years ($F = 6.26$; $df = 3, 120$; $P = 0.0006$) (Fig. 3).

Trends across and between years

Over the four-year study, damage ratings varied between species ($\chi^2 = 125.19$, $df = 1$, $P < 0.0001$) and years ($\chi^2 = 960.38$, $df = 3$, $P < 0.0001$). Moreover, the degree of susceptibility of the different species changed depending on the year ($\chi^2 = 31.68$, $df = 1$, $P < 0.0001$) (Fig. 4). Damage from mites was most abundant in the first year of the study, with mean ratings of 2.79 (± 0.04 SEM). The final year of the study, 2020, had the lowest mean ratings at 1.66 (± 0.04), compared to 2018 at 2.09 $\pm$ (0.04) and 2019 at 2.00 (± 0.04). In each of the four years, hybrid plants had higher damage ratings than *C. americana* plants (Table 1; Fig. 4), with many models indicating that hybrid plants had an average damage rating between 0.1–0.8 points higher than *C. americana* plants after accounting for any additional spatial effects (coefficients for species term in Table 1).

Table 1. Summary of simultaneous autoregressive models for ratings of *P. avellanae* infestation on hazel plants in a mixed-species hazelnut field in Wisconsin from 2017-2020. Numbers indicate the model coefficients $\pm$ SE and their respective *P* values in parentheses. The term for Species represents a binomial

variable (i.e., 1 represents hybrid and 0 represents *C. americana*). The best model for each year is presented in the bottom row of each year's section.

Year	Intercept	Species	Local trend		Field-based trends				AIC	Δ AIC
			Rook	Northing	Easting	N×E	Northing ²	Easting ²		
2017	1.839 ± 0.096 (<0.0001)								2113	
	1.329 ± 0.146 (<0.0001)	0.274 ± 0.059 (<0.0001)							2094	19
	0.570 ± 0.073 (<0.0001)		0.194 ± 0.009 (<0.0001)						2039	74
	0.306 ± 0.137 (0.026)	0.470 ± 0.084 (<0.0001)	0.118 ± 0.014 (<0.0001)	0.008 ± 0.003 (0.0018)	0.079 ± 0.279 (0.0044)			-0.004 ± 0.001 (0.0028)	2001	112
	2.737 ± 0.068 (<0.0001)								2278	
2018	2.278 ± 0.143 (<0.0001)	0.217 ± 0.060 (0.0003)							2267	11
	1.906 ± 0.142 (<0.0001)		0.088 ± 0.014 (<0.0001)						2263	15
	0.954 ± 0.217 (<0.0001)	0.798 ± 0.095 (<0.0001)	0.045 ± 0.015 (0.0029)	0.019 ± 0.006 (0.0014)	-0.008 ± 0.036 (0.8132)	-0.001 ± 0.000 (0.0215)		0.004 ± 0.001 (0.0051)	2171	107
	2.022 ± 0.052 (<0.0001)								2186	
	1.575 ± 0.123 (<0.0001)	0.206 ± 0.051 (<0.0001)							2173	13
2019	1.136 ± 0.099 (<0.0001)		0.123 ± 0.013 (<0.0001)						2151	35
	0.995 ± 0.109 (<0.0001)	0.495 ± 0.081 (<0.0001)	0.094 ± 0.013 (<0.0001)						2118	68
	1.762 ± 0.040 (<0.0001)								4166	
	1.579 ± 0.094 (<0.0001)	0.084 ± 0.039 (0.031)							4164	2
	0.797 ± 0.061 (<0.0001)	0.151 ± 0.009 (<0.0001)							4024	142
2020	0.912 ± 0.122 (<0.0001)	0.386 ± 0.063 (<0.0001)	0.158 ± 0.010 (<0.0001)	-0.018 ± 0.007 (0.0158)	-0.053 ± 0.014 (0.0001)		0.000 ± 0.000 (0.0151)	0.003 ± 0.001 (0.0002)	3976	190

Spatial trends

We noticed two types of spatial trends in damage ratings. First, we observed strong localized trends, or hot-spots, in *P. avellanae* damage ratings each year (i.e., significance of rook's case term in models in Table 1). That is, a plant with higher damage ratings was frequently surrounded by other plants with higher damage levels as well. Second, after accounting for differences in *P. avellanae* ratings between species and hot-spots, there were still field-level spatial trends (i.e., terms for northing, easting, etc.) in most years. These larger, field-level trends were not the same every year, as the estimates of model coefficients varied across years (Table 1). Ratings increased towards the north end of the field in 2017 and 2018, indicating an edge effect on the north side of the field in those two years (Table 1; Fig. 5a, b). No field-level spatial trends were observed in 2019 (Table 1; Fig. 5c). In 2020, however, *P. avellanae* ratings increased towards the south end of the field (Table 1; Fig. 5d). Ratings also increased towards the east end of the field in 2018 but then increased towards the west in 2020 (Table 1; Fig. 5b, d). Additionally, *P. avellanae* ratings increased towards the center of the field in 2017, 2018 and 2020 (Table 1; Fig. 5a, b, d).

In summary, the significant and dynamic field-based spatial trends in three of the four years of the study indicate that *P. avellanae* distribution and severity can change from year to year within a field.

Discussion

Our finding that ratings of *P. avellanae* infestation were higher on hybrid than American hazels each year did not support our initial hypothesis (Table 1; Fig. 3). Previous findings from Oregon and New York found two cultivars of the American hazel, 'Rush' and 'Winkler', were highly susceptible to *P. avellanae* infestation; a trait thought to be passed onto their hybrid progeny (Ourecky and Slate 1969; Thompson 1977; Chen et al. 2007). However, two other reports indicate a wide range of *P. avellanae* susceptibility in wild populations of beaked hazelnut in the United States (Brenner 1986; Thompson et al. 1996). We suspect that phenological and physical differences between plants could play a major role in susceptibility to *P. avellanae*.

Phytoptus avellanae has a life cycle like that of other eriophyid gall-forming mites (Keifer 1946; Fig. 1). *Phytoptus avellanae* only colonizes new buds formed during the mites' migration period, during which hazel plants or cultivars with looser bud scale morphology may be more susceptible to *P. avellanae* infestation (Krantz 1974; Thompson 1977; Burgess 1983; Burgess and Thompson 1985). The *C. americana* plants in our study have different bud morphology and phenology compared to the hazel hybrids; we observed that pollination, bud formation, bud opening, and nut formation in *C. americana* plants occurs several weeks earlier than hybrid (HNS personal observation). These phenomena could explain why hybrids had higher damage ratings for *P. avellanae* than American hazel plants in our study, as buds on the American hazel plants appeared both tighter and earlier to open than most hybrids (HNS, personal observation). Additionally, this result shows some promise that wild American hazel stands in the Upper Midwest may be resilient against the invasive *P. avellanae* and that interplanting of American hazel within hybrid hazel field may deter mite spread and proliferation within the field. However, surveys of wild *C. americana* stands need to be conducted to confirm this conjecture, especially near nurseries and orchards where hybrid hazels are grown that may harbor *P. avellanae*.

Conducting this study in an established hazel germplasm planting across four successive years in a novel geographic location for the pest provided the opportunity to measure within-field spatial patterns of *P. avellanae* and differences in infestation between hazel species. Our results that *P. avellanae* distribution and damage severity change from year to year within a field while hot-spots are present annually suggest that *P. avellanae* moves between adjacent plants (Table 1; Fig. 5). Eriophyid mites can disperse by walking between adjacent plants, wind currents, and via phoresy (Jeppson et al. 1975; Sabelis and Bruin 1996). We view it as unlikely that annual ingress was occurring from surrounding areas. There are not wild hazelnuts in the proximal surrounding landscapes of this planting that could be considered sources of filbert bud mites. We did not observe consistent edge effects in our study that might be expected from a migration gradient. Higher ratings of *P. avellanae* infestation towards the

middle of the field in most years, as shown in Fig. 5, suggests that whole fields of hazels may need to be scouted for *P. avellanae* damage rather than focusing on field edges. However, outbreaks of *P. avellanae* within a field will most likely occur near other highly infested plants.

The higher ratings of *P. avellanae* infestation in 2018 compared to other years is likely relate to climatic suitability (Fig. 3, 5). The migration of mass numbers of nymphs of *P. avellanae* from previously infested buds to newly formed auxiliary buds begin in spring once maximum and mean daily temperatures exceed 15 °C and 9 °C, respectively (Özman and Toros 1997a; Webber et al. 2008; Fig. 1). High temperatures and heavy rain, however, can cause high mortality of migrating nymphs, leading to reduced infestations noted in subsequent years (Özman and Toros 1997a; Webber et al. 2008). Our temperature analysis showed that the month of May exhibited higher daily mean temperatures in 2018 than other years, which is a key first month of nymphal *P. avellanae* migration (Fig. 1, 3). Moreover, while our weather analysis showed no differences between precipitation between years, the historical state-wide public data for Bayfield County, Wisconsin shows excess precipitation in 2017 and abnormally dry conditions for May 2018 and the summer of 2019 (Svoboda et al. 2002; Koch and Coulton 2019; NIDIS 2023; SI 1). The precipitation analysis between months shows that June 2018 had much higher rainfall than in other years (Fig. 3). Furthermore, during the estimated 90-day nymphal migration period in 2018, there were ten days of heavy rainfall (i.e., over 4 mm of rain per hour), with five days experiencing over seven hours of heavy rainfall (SI 2). Besides the amount of rain, 2018 had 29 days over 27 °C during this period. Thus, more than one third of the migration period exhibited high mortality factors for nymphs (SI 2). Additionally, 2019 exhibited the lowest overall winter temperatures, which may cause considerable mortality of the mites (Sabelis and Bruin 1996; Fig. 3). High frequency of mortality factors during nymphal migration in 2018 and early 2019 likely reduced populations and led to decreased damage ratings for the springs of 2019 and 2020 (Fig. 5). According to the results of this and other studies, climatic conditions play an important role in the success of mite migration and dispersion (Beber 1994; Sabelis and Bruin 1996; Özman and Toros 1997a). However, there are other possible factors, not studied yet for hazelnut, that may influence *P. avellanae* populations and distribution such as physiological and chemical responses of differing hazel species and genotypes to mite herbivory.

With the establishment of a hazelnut industry in the Upper Midwest underway, understanding the severity and dynamics of pest complexes is crucial to its early success. The lower susceptibility of American hazel plants vs. established hazel hybrids suggests that the former show promise as parents in hybrid breeding efforts for resistance to *P. avellanae*. The spatial and temporal trends suggest that mite sampling protocols, when developed for eventual selections, will need to consider multiple levels of scale, and may be improved by accounting for anomalies in spring weather patterns between years. Overall, the findings of our study provide insight on the dispersal, within field distribution and host-plant preferences of *P. avellanae* that will contribute to preventative and cultural control of this harmful pest.

Declarations

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Conflicts of interest

The authors have no relevant financial or non-financial interests to disclose.

Availability of data and material

The datasets generated during and analyzed during the current study are available upon request.

Code availability

The code generated during analysis of the datasets used in this study are available upon request.

Author Contribution Statement

JAF and AC conceived research, established research site and coordinated data collection. BHA provided guidance on statistical analysis interpretation. HNS performed formal statistical analysis and investigation. HNS prepared the original draft of the manuscript and created all figures. JAF, BHA and HNS acquired funding for the research. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

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Figures

Autumn and Winter

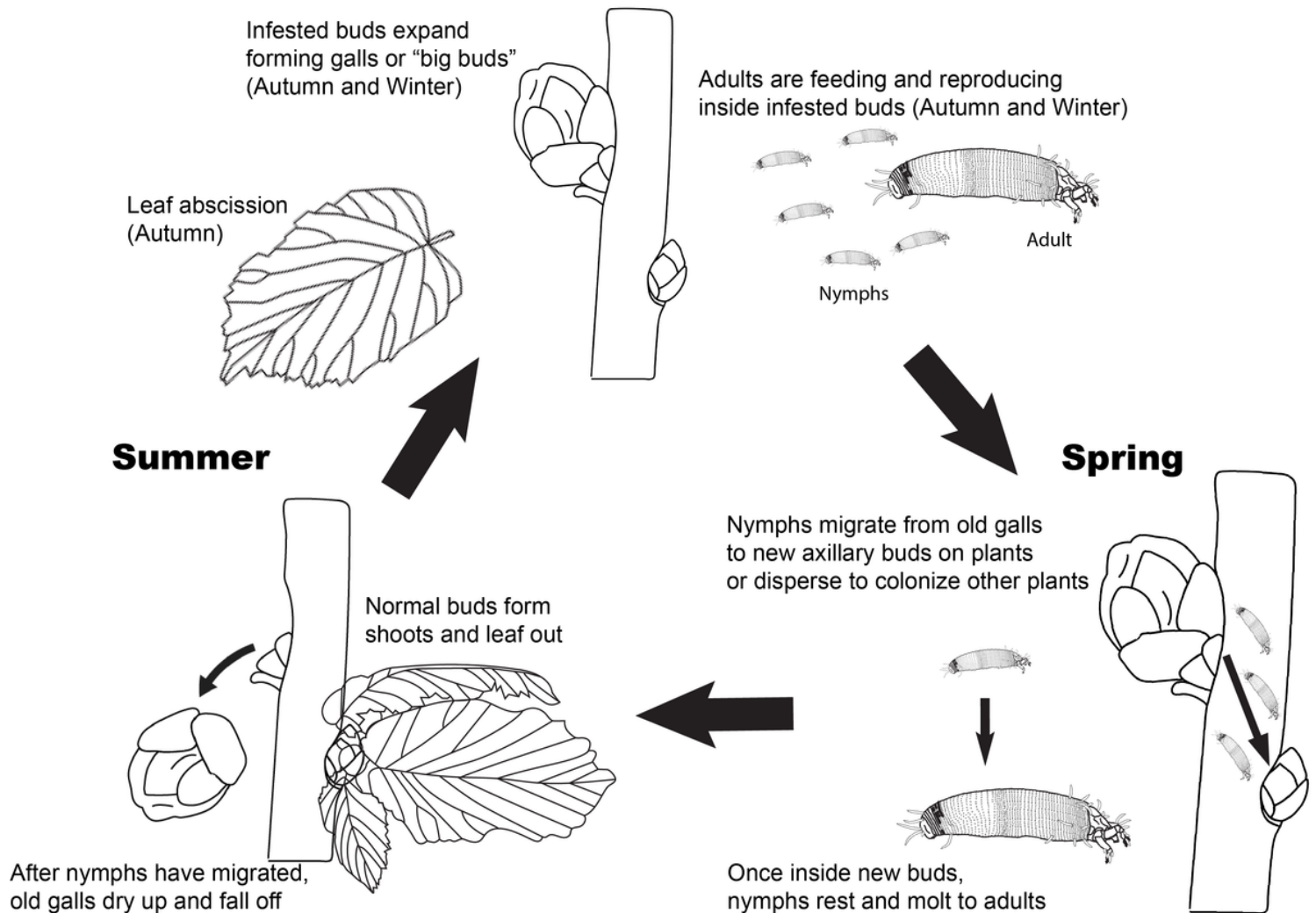


Figure 1

Representation of the life cycle of *Phytoptus avellanae* in Wisconsin, USA. In spring, between late-April and early-July, over an approximately 90-day period, nymphs continually migrate by walking from existing galls or "big buds" to axillary newly formed buds on the hazel plant or by dispersing via wind or phoresy to buds on other hazel plants. Once inside the new bud, nymphs enter a resting period which lasts about a month; the timing of the resting periods vary for nymphs depending on when they migrated from the previous gall. After the resting period, nymphs eclose as adults and reproduction begins until the following spring and feeding continues inside the newly infested bud leading to the formation of a new gall. Newly formed galls can be observed as early as late-summer after the nymphal migration.

Illustration by HNS.

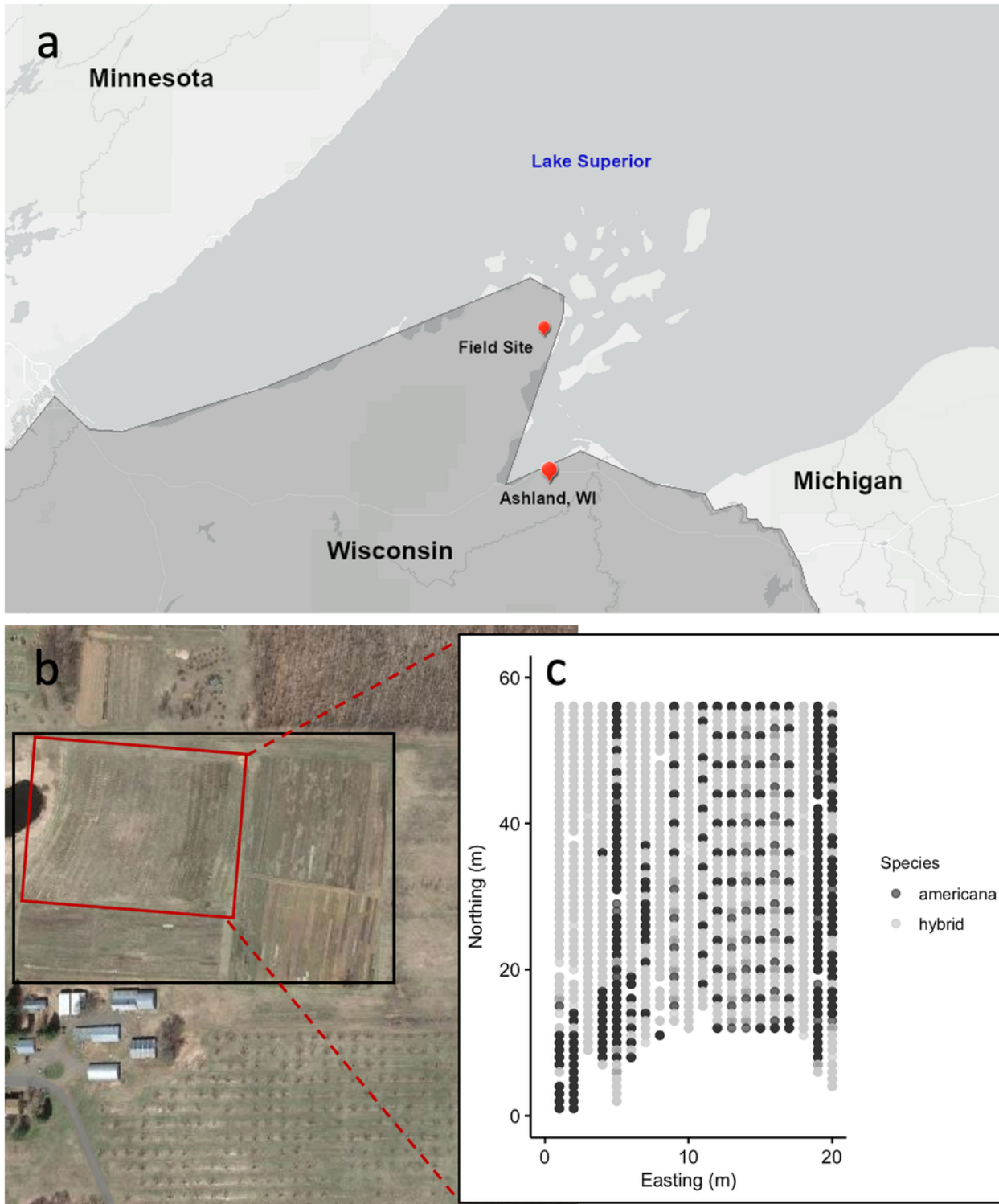


Figure 2

Maps of the field site in Bayfield, Wisconsin in 2017: a) a map showing where the field site and weather station are located within Wisconsin, represented by red points, b) an aerial satellite image of the field site with the whole hybrid hazelnut planting outlined in black and section used for the study outlined in red; and c) a map of the planting by *Corylus* species with dots representing individual hazel plants. Note that

the section of the hybrid hazelnut planting used for the study was chosen for representative, established plants; the other sections are comprised of newly planted, young plants only.

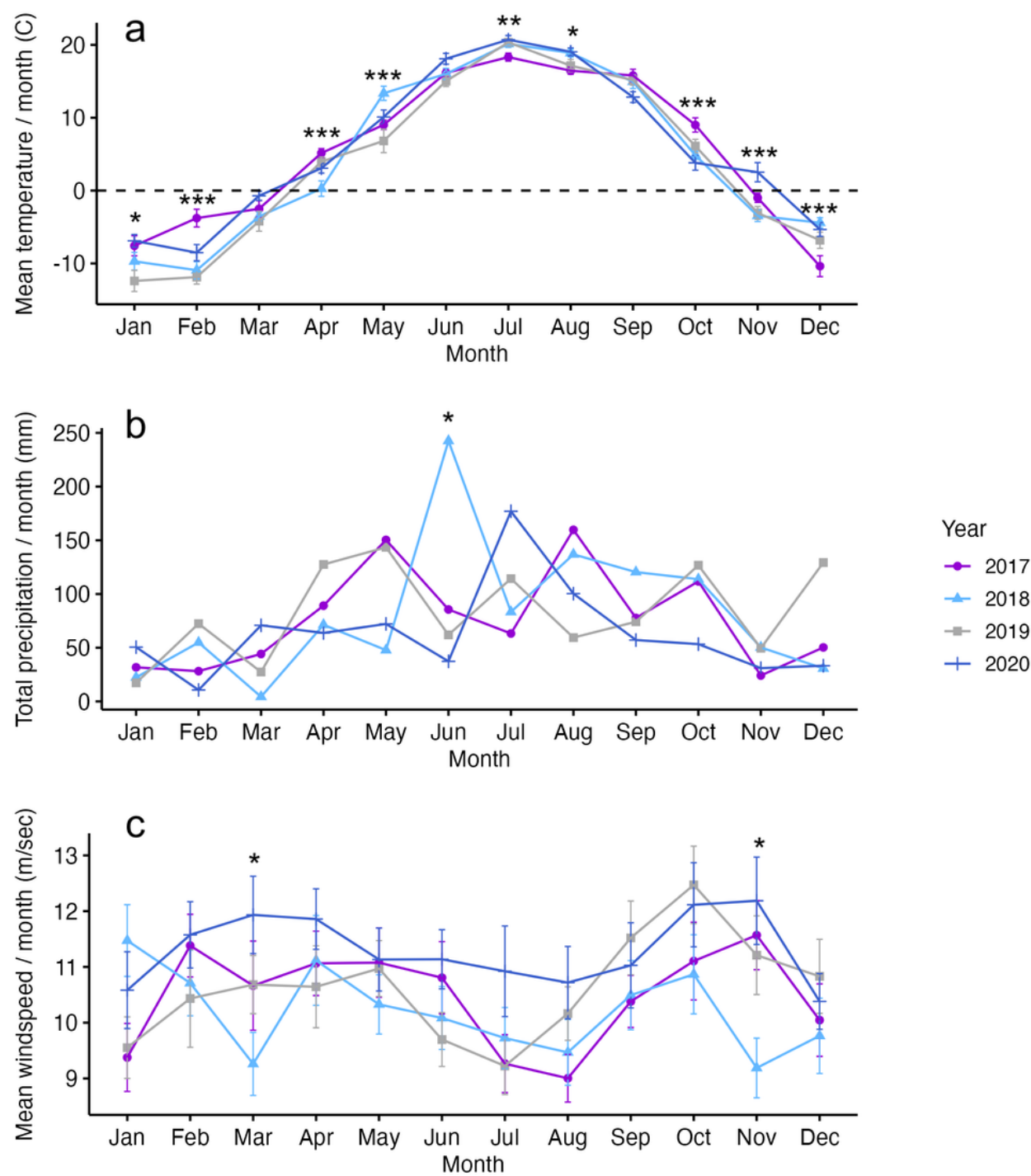


Figure 3

Mean monthly a) temperatures in C° ± SEM, b) precipitation in centimeters ± SEM, and c) fastest five-second windspeed in meters per second ± SEM from a weather station in Ashland County, Wisconsin (46°

32' 48.3354"N, -90° 55' 6.42"W) for 2017-2020. Asterisks above a specific month represent significant differences between years where '*' represents a *P* value at the 0.05 significance level, '**' represents the 0.01 significance level, and '***' represents the 0.001 significance level.

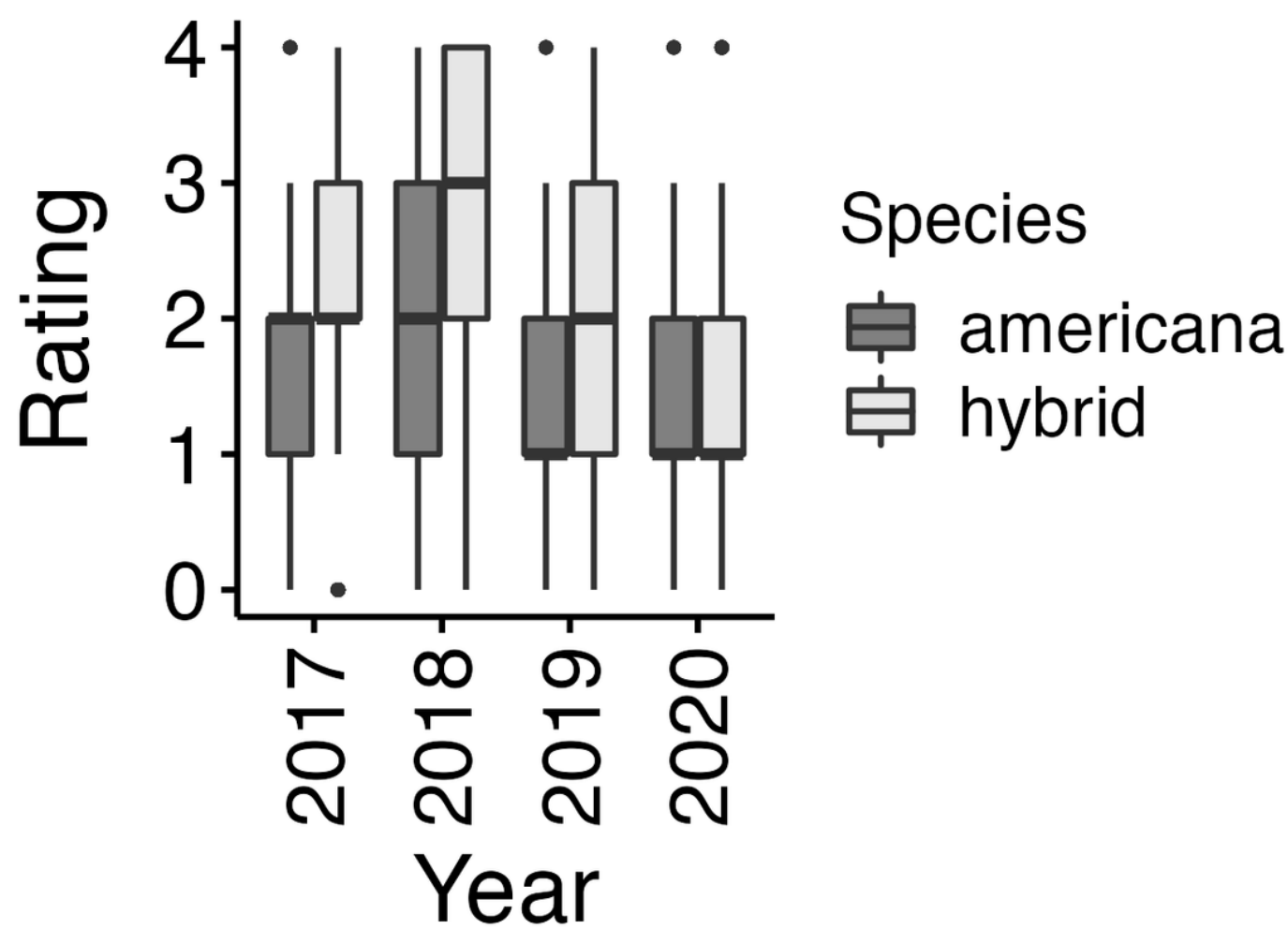


Figure 4

Box and whisker plot of ratings for *Phytoptus avellanae* damage in 2017, 2018, 2019, and 2020 by species of hazel in a hazelnut field in Bayfield, Wisconsin. All individual hazels were surveyed for galls caused by *P. avellanae* and assigned a qualitative damage rating of 0 through 4, with 0 representing 0% of the plant's buds galled, 1 representing 1-25%, 2 representing 26-50%, 3 representing 51-75%, and 4 representing 76-100% of the plant's buds galled respectively. The upper whisker indicates the third quartile added to $1.5 \times$ the interquartile range. The lower whisker represents the first quartile minus $1.5 \times$ the interquartile range. Dots represent data points. Asterisks above each pair of boxplots indicate significant differences within years at $P < 0.05$.

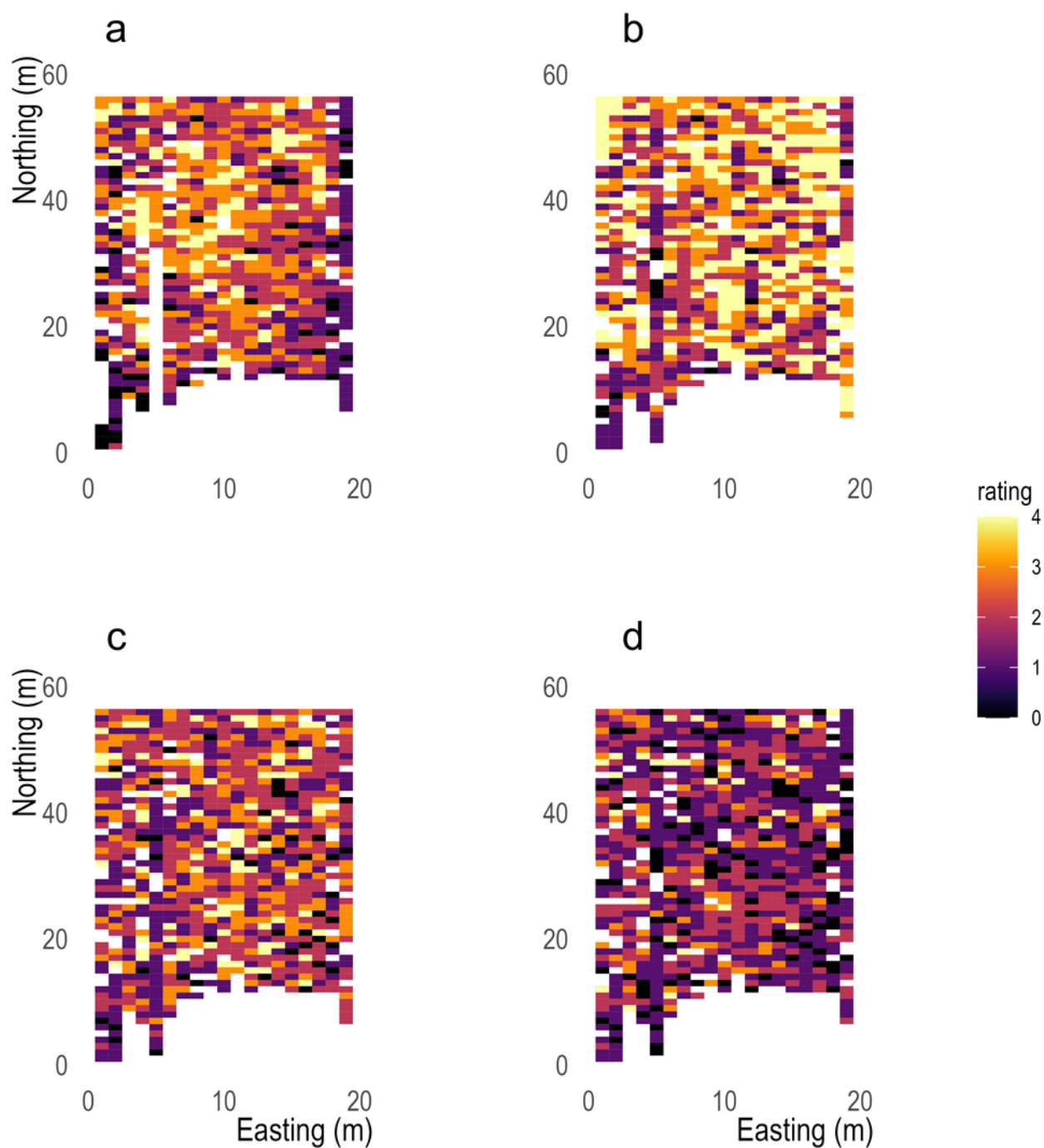


Figure 5

Heat maps of *P. avellanae* damage ratings in a) 2017, b) 2018, c) 2019, and d) 2020. All individual hazels were assigned a rating of 0 through 4, with 0 representing 0%, 1 representing 1-25%, 2 representing 26-50%, 3 representing 51-75%, and 4 representing 76-100% of the plant's buds were galls respectively. Individual tiles represent individual hazelnut plants in the field. White tiles indicate a rating was not given for a plant due to coppice status or death of the plant in that year.

Supplementary Files

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