Ecology, 94(12), 2013, pp. 2792–2802

Effects of plant genotype and insect dispersal rate on the population dynamics of a forest pest

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Abstract. It has been shown that plant genotype can strongly affect not only individual herbivore performance, but also community composition and ecosystem function. Few studies, however, have addressed how plant genotype affects herbivore population dynamics. In this paper, we used a simulation modeling approach to ask how the genetic composition of a forest influences pest outbreak dynamics, using the example of aspen (*Populus tremuloides*) and forest tent caterpillars (FTC; *Malacosoma disstria*). Specifically, we examined how plant genotype, the relative size of genotypic patches, and the rate of insect dispersal between them, affect the frequency, amplitude, and duration of outbreaks. We found that coupling two different genotypes does not necessarily result in an averaging of insect dynamics. Instead, depending on the ratio of patch sizes, when dispersal rates are moderate, outbreaks in the two-genotype case may be more or less severe than in forests of either genotype alone. Thresholds for different dynamic behaviors were similar for all genotypic combinations. Thus, the qualitative behavior of a stand of two different genotypes can be predicted based on the response of the insect to each genotype, the relative sizes of the two patches, and the scale of insect dispersal.

Key words: aspen; forest tent caterpillar; genotype; Malacosoma disstria; *outbreak; parasitoid; population dynamics;* Populus tremuloides; *simulation model; spatial heterogeneity*.

Introduction

It is increasingly recognized that plant genotype plays an important role in shaping associated animal populations and communities. Much of the current emphasis, however, has focused on static measures such as herbivore performance (Hwang and Lindroth 1997, Lindroth et al. 2002, Holton et al. 2003, Kopper and Lindroth 2003), abundance, and community composition (Bailey et al. 2006, Bangert et al. 2006, Bangert 2008, Barbour et al. 2009). While plant genotype is known to affect herbivore performance through differences in the concentration of nutrients and defensive compounds (Hemming and Lindroth 1995, Hwang and Lindroth 1997, Cronin and Abrahamson 1999, Underwood and Rausher 2000, Lindroth et al. 2002, Holton et al. 2003, Kopper and Lindroth 2003, Johnson 2008), few studies have addressed the role of plant genotype as a determinant of herbivore population or community dynamics, and none have examined long-term oscillatory dynamics (Underwood and Rausher 2000, McIntyre and Whitham 2003, Underwood 2004, 2009, Johnson 2008). Some of the most dramatic instances of dynamics in herbivore populations are the periodic outbreaks of forest insects. Whether and how plant genotype affects insect outbreak characteristics, including severity, frequency, and duration, remains an open question. If certain plant genotypes or combinations of genotypes make outbreaks more severe or more frequent, then understanding the interplay between plant genotype and pest outbreaks is important for both basic ecology and management.

In this paper, we used a simulation modeling approach to ask how the genetic composition of a forest influences the outbreak dynamics of an herbivorous insect. Specifically, we investigated the role of plant genotype, genotypic patch sizes, and the rate of dispersal between patches. The model was developed and parameterized using data from a tri-trophic system comprised of quaking aspen (*Populus tremuloides*), forest tent caterpillars (FTC; *Malacosoma disstria*), and FTC parasitoids. We selected this system because there are empirical data describing individual-level FTC performance on different aspen genotypes (Hemming and Lindroth 1995, Hwang and Lindroth 1997, Holton et al. 2003, Kopper and Lindroth 2003) and linking these individual measures to demographic rates (Parry et al. 2001, Cobbold et al. 2009). The model allowed us to scale-up from the individual level to larger scale FTC population dynamics.

Manuscript received 3 October 2012; revised 24 May 2013; accepted 29 May 2013; final version received 19 June 2013. Corresponding Editor: N. Underwood.

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Spatial heterogeneity is a prominent feature of many ecological systems, and has been shown to affect population dynamics. For example, many studies have examined how fragmented landscapes can lead to synchrony or asynchrony. Typically, these studies consider cases in which patches with the same (mean) demographic parameters (including the intrinsic population growth rate, r, or carrying capacity, K) are linked by varying levels of dispersal (Comins et al. 1992, Ruxton and Rohani 1996, Heino et al. 1997, Ranta et al. 1998). When demographic parameters are homogeneous, a small amount of dispersal is often sufficient for synchrony to develop (Ranta et al. 1998). However, even when patches are identical, certain combinations of host and predator/parasitoid dispersal can lead to systematically out-of-phase dynamics (Koelle and Vandermeer 2004). A few studies have also addressed spatial heterogeneity that includes underlying differences in patch quality, represented by differences in r (Kendall and Fox 1998) or K (Ylikarjula et al. 2000, Engen et al. 2002). In this case, the dynamics can be more complex, and higher levels of dispersal may be required for synchrony than in the homogeneous case (Kendall and Fox 1998, Goldwyn and Hastings 2009). In the case of herbivorous insects, heterogeneity in demographic rates could arise from variation in exposure to predators (Hassell and May 1988, Nachman 2001, McGeoch and Price 2005, Heard et al. 2006, Haynes et al. 2013) or differences in plant quality (Helms and Hunter 2005, Cornelissen and Stiling 2006, Jactel and Brockerhoff 2007, Underwood 2007, Charbonneau et al. 2012).

In our model, patch differences in insect demographic rates are the result of differences between plant genotypes. There are two features of the aspen–FTC–parasitoid system that make it particularly useful for investigating the role of genetically-based spatial heterogeneity. First, more is known about the relationships between individual FTC performance, the effect of plant genotype on individual performance, and key demographic rates than in most insect species. Specifically, FTCs raised on different aspen genotypes differ both in pupal mass and in time to pupation (Hemming and Lindroth 1995, Orians et al. 1996, Hwang and Lindroth 1997, Holton et al. 2003, Kopper and Lindroth 2003, Stevens and Lindroth 2005). Female pupal mass is positively correlated with the number of eggs laid (Parry et al. 2001), and thereby the intrinsic rate of population growth. FTC time to pupation influences parasitoid survival (Cobbold et al. 2009), thus affecting the timing and extent of outbreak quenching by parasitoids. Second, aspen grow clonally, with single genotypes forming large discrete patches ranging from a few square meters to several hectares in size (Sakai and Burris 1985, Mitton and Grant 1996). This considerably simplifies the genotypic composition of aspen systems relative to other forests, and makes the application of a patch-based model particularly appropriate.

When demographic rates differ between clonal patches, and patches are isolated or very weakly linked, we expect different dynamics on each patch. With increasing amounts of dispersal, however, patch dynamics should become synchronized and of similar magnitude over a wider geographic area (Bjornstad et al. 1999). When and how this occurs, and how it depends on patch size, remain open questions, although it is known that synchrony in FTC outbreaks is lower in the prairie provinces of Canada where forests are more fragmented (Cooke et al. 2009). It is also unclear how forest composition will affect outbreak characteristics including frequency, severity, and duration. On the one hand, it is reasonable to assume that a mixed forest could exhibit outbreaks that are intermediate in frequency, severity, and duration as compared to a forest composed of each individual clone. However, Underwood (2009) found that the effects of plant genotype on aphid population dynamics were nonadditive, and other studies have shown that increased host plant genetic diversity may either decrease (Perrin 1977, Power 1988, Peacock et al. 2002, Hajjar et al. 2008) or increase (Kotowska and Cahill 2009, Utsumi et al. 2011, Castagneyrol et al. 2012) herbivore abundance. Thus, outbreak severity could also be reduced or exacerbated in mixed-genotype forests relative to single-genotype forests.

To address the question of how genotypic heterogeneity alters outbreak dynamics, we began with a basic model of FTC population dynamics developed by Cobbold et al. (2009). Parameterizing this model using aspen genotype-specific FTC performance measurements (Holton et al. 2003, Kopper and Lindroth 2003) and the relationship between pupal mass and fecundity (Parry et al. 2001), we explored the predicted effect of aspen genotype on outbreak characteristics in isolated single-genotype stands. We then extended the model to consider two-patch scenarios where different clonal stands are connected by insect dispersal. Although our model was developed for aspen forests, it could easily be extended to any ecosystem dominated by clonal plants, such as grasslands (Eriksson 1989) and wetlands (Barrett et al. 1993, Amsberry et al. 2000, Pennings and Callaway 2000), as well as in agricultural or silvicultural landscapes where large areas are planted with genetically similar individuals (Karnosky 1981, Andow 1983, Zhu et al. 2000, Park 2002).

Methods

The aspen–FTC–parasitoid system

Quaking aspen (*Populus tremuloides*) is the second most widespread tree species in the world (Mitton and Grant 1996), with a range extending across Canada and down into the Rocky Mountains, the Great Lakes states, and the Northeast USA. It is frequently managed for wood and pulp production (David et al. 2001). High levels of genetic diversity have been measured both within and between populations (Mitton and Grant

1996), and genotypes (clones) can differ substantially in many traits, including the levels of defensive compounds and nitrogen in foliage (Lindroth and Bloomer 1991, Hemming and Lindroth 1995, Hwang and Lindroth 1997). Phenolic glycoside levels in *P. tremuloides* can range from 1% to 19% dry mass; higher levels are associated with slow development and low mass gain in several insect species (Hemming and Lindroth 1995, Hwang and Lindroth 1997, Holton et al. 2003, Kopper and Lindroth 2003). Because phenolic glycosides are not induced by defoliation during the FTC developmental period (Osier and Lindroth 2004, Stevens and Lindroth 2005), the difference in defenses between genotypes is maintained regardless of FTC population density. Clonal patches tend to be discrete, rather than overlapping (Sakai and Burris 1985, Mitton and Grant 1996).

Forest tent caterpillars (*Malacosoma disstria*) are native to North America. As a species, FTC are host generalists, but populations tend to specialize on one or two broadleaf tree species (Parry and Goyer 2004). The primary host in the north is quaking aspen (Lindroth and Bloomer 1991, Roland 1993, Parry and Goyer 2004). FTC undergo roughly periodic population cycles (Hodson 1941, Cooke and Lorenzetti 2006), and outbreaks can defoliate tens of thousands to more than one million hectares, reducing productivity and timber yields (Anon 1991, Roland 1993, Fitzgerald 1995). Outbreaks occur every 7 to 19 years and last 2 to 5 years (Cobbold et al. 2009). These cycles are driven in large part by interactions with parasitoids, though climatic variation also plays a role (Roland and Taylor 1997, Roland 2005). The primary parasitoid species varies across the FTC range, but can include several wasp and fly species such as *Aleiodes malacosomatus*, *Leschenaultia exul*, *Carcelia malacosomae*, *Patelloa pachypyga*, and *Arachnidomya aldrichi* (Cobbold et al. 2009). Both FTC and its parasitoids are univoltine.

Model

System dynamics.—We modeled FTC dynamics in a single-genotype aspen stand using the modified Nicholson-Bailey model developed in Cobbold et al. (2009). We then examined FTC dynamics in a mixed-genotype aspen stand by extending the model to consider two geographically separate patches, representing distinct aspen genotypes. Patches are connected through the movement of adult moths and/or parasitoids prior to egg-laying. When dispersal is equal to zero, the model reduces to two single-patch cases. The model was written and implemented in MATLAB (MathWorks 2012).

FTC larval performance has been measured on three aspen clones planted at the Aspen FACE (free-air carbon dioxide enrichment) site in Rhinelander, Wisconsin, USA (Holton et al. 2003, Kopper and Lindroth 2003). Because larvae had the highest final pupal mass and fastest development on clone 259, the lowest pupal mass and slowest development on clone 216, and intermediate pupal mass and development time on clone 271, we will hereafter refer to 259 as the "high-quality" clone, 216 as the "low-quality" clone, and 271 as the "medium-quality" clone. Based on mass and development time, we estimated FTC growth rate (r), and parasitoid survival (α) on each clone (see section entitled *Parameter values* below and Table 1). In addition, we assumed that the size of each clonal patch can vary, such that the area of patch 2 is β times the area of patch 1.

The density of FTC cocoons in patch 1 in year t is denoted by $H_{1,t}$ and the corresponding density in patch 2 by $H_{2,t}$. Density is scaled by the carrying capacity of the patch, such that H ranges between 0 and 1. We assumed that caterpillar performance differs between clones, but the maximum number per unit area (carrying capacity) does not. After pupation, a proportion m_h of adults disperse to the other patch (host migration rate). Post-dispersal FTC densities are

$$H'_{1,t} = H_{1,t} - m_h H_{1,t} + m_h \beta H_{2,t}$$
$$H'_{2,t} = H_{2,t} - m_h H_{2,t} + m_h \frac{1}{\beta} H_{1,t}. \quad (1a)$$

Notice that β appears in these equations because, although both patches lose the same proportion of the population to dispersal, the effect on the density of the receiving patch is determined by the relative sizes of the two patches. Similarly, for parasitoids ($P_{1,t}$ and $P_{2,t}$) with dispersal rate m_p (parasite migration rate) the post-dispersal densities are given by

$$P'_{1,t} = P_{1,t} - m_p P_{1,t} + m_p \beta P_{2,t}$$
$$P'_{2,t} = P_{2,t} - m_p P_{2,t} + m_p \frac{1}{\beta} P_{1,t}. \quad (1b)$$

Once the insects are settled in a patch, reproduction, density-dependent mortality, and parasitism occur according to a modified Nicholson-Bailey model (Cobbold et al. 2009):

$$H_{1,t+1} = H'_{1,t} e^{r} e^{-\mu(H'_{1,t})} f(P'_{1,t})$$
$$H_{2,t+1} = H'_{2,t} e^{r} e^{-\mu(H'_{2,t})} f(P'_{2,t})$$
$$P_{1,t+1} = H'_{1,t} e^{-\alpha\mu(H'_{1,t})} [1 - f(P'_{1,t})]$$
$$P_{2,t+1} = H'_{2,t} e^{-\alpha\mu(H'_{2,t})} [1 - f(P'_{2,t})]. \quad (2)$$

In Eq. 2, the FTC populations exhibit Ricker density dependence and the fraction of FTCs surviving density-dependent competition is given by $e^{-\mu(H_{i,t})} = e^{-r_i H_{i,t}/K}$, where K is the carrying capacity. In addition, FTCs must evade parasitism. Assuming that parasitoid attacks are distributed according to the zero term of the negative binomial distribution, FTCs will evade parasitoids with probability

$$f(P'_{i,t}) = \left(1 + \frac{aP'_{i,t}}{k}\right)^{-k}$$

TABLE 1. Forest tent caterpillar (*Malacosoma disstria*) population growth rate (r) and parasitoid survival parameter (α) on each quaking aspen (*Populus tremuloides*) genotype.

Genotype	r	α
"Low-quality" clone 216	0.458	0.5247
"Medium-quality" clone 271	0.548	0.6323
"High-quality" clone 259	0.644	0.7455

Notes: Parasitoid survival parameter, α, assumes a parasitoid emergence time (PET) of 37 days after caterpillar hatching. See *Methods: Model: System dynamics* for a description of the aspen clones.

where a is the searching efficiency of the parasitoid, and k is the degree of clumping of parasitoid attacks. Parasitoids must also survive density-dependent competition among FTCs. If parasitoids emerge later, the number of parasitoids emerging is reduced due to prior density-dependent mortality of the caterpillar hosts. The fraction of parasitoids surviving density dependent competition amongst FTCs is given by $e^{-\alpha_i \mu(H_i)}$. The parameter that scales parasitoid survival with emergence time is $\alpha \leq 1$.

Parameter values.—The primary effect of aspen genotype on caterpillar dynamics is to alter caterpillar time to pupation and pupal mass (Appendix A: Table A1). Table 1 shows the values of α and r estimated for each of the aspen clones in our study. These values of α assume a parasitoid emergence time (PET) of 37, where PET is defined as the day of caterpillar development on which the parasitoid emerges. For a given PET, differences in caterpillar development rate can change the FTC life stage from which the parasitoid emerges, and hence parasitoid survival (Fig. 1). More details regarding the estimation of these and other parameters can be found in Appendix B.

Numerical method.—Eqs. (1) and (2) were simulated for 40 000 years; the first 20 000 years were discarded to avoid transient dynamics. Oscillatory behavior was analyzed using the second 20 000-year time series. The frequency of population fluctuations was calculated using a fast Fourier transform. FTC or parasitoid dynamics were considered fully synchronized if peak insect abundance occurred in the same year for both patches. Average outbreak duration was calculated as time spent above 50% carrying capacity. Unless otherwise stated, we assumed that the parasitoid dispersal rate was half the FTC dispersal rate. Because FTCs are larger than their parasitoids, it seemed reasonable to assume that they would be able to disperse farther (Roland 1993). However, in Appendices C and D, we show results for different ratios of host to parasitoid dispersal, as well as for earlier and later parasitoid emergence times (PETs). Some variation in dispersal ratios and PET is expected in real systems depending on which parasitoid species is dominant in any given area.

RESULTS

How does plant genotype affect outbreak frequency and peak abundance?

In Fig. 2, we show FTC outbreak frequencies and peak host abundance on isolated stands of high- (259), medium- (271), and low-quality (216) aspen clones as a function of parasitoid emergence times. For PETs <25

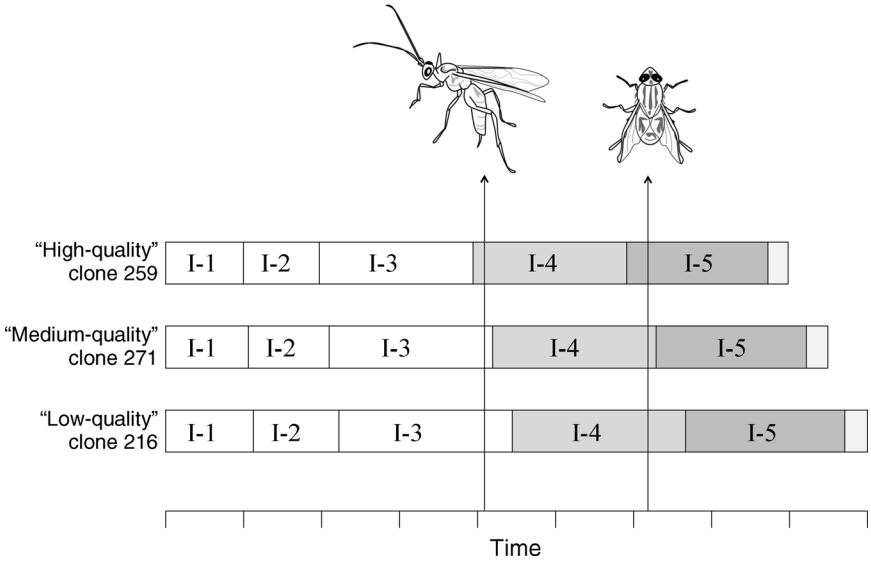

FIG. 1. Lengthening or shortening forest tent caterpillar (FTC; *Malacosoma disstria*) development time can change the relationship between host and parasitoids by causing parasitoids to emerge at different host life stages (arrows). This is true whether the parasitoid is an early-emerging species (such as the wasp *Aleiodes malacosomatus*) or a late-emerging species (such as the fly *Leschenaultia exul*). I-1 denotes FTC instar 1, I-2 instar 2, and so on. The final blank box represents the pre-pupal stage. See *Methods: Model: System dynamics* for a description of the quaking aspen (*Populus tremuloides*) clones. The actual time is arbitrary, and therefore unitless.

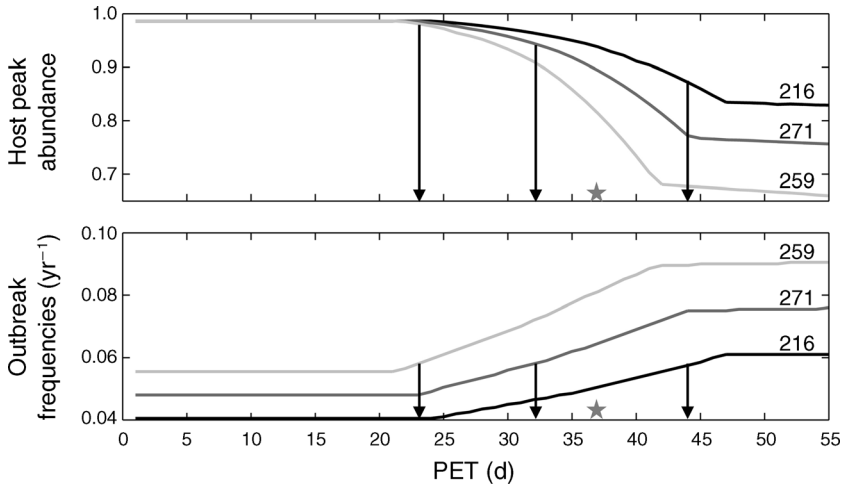

FIG. 2. FTC peak abundance and outbreak frequency predicted by single-patch model for each genotype (light gray shows the "high-quality" clone 259, medium gray is the "medium-quality" clone 271, black is the "low-quality" clone 216) for a range of parasitoid emergence times (PET). Abundance is defined as the proportion of the total carrying capacity. Arrows indicate values of PET for which outbreak frequency would be the same on all three genotypes (0.06); notice that the peak abundances for these PET values differ (top). The star indicates a PET of 37 days, the value used in subsequent analyses.

days, the FTC peak abundance on all clones is similarly high. As PET increases, peak abundances diverge, with higher peak abundance on the lower quality clones. However, provided parasitoid emergence times did not change in response to aspen genotype, FTC outbreaks will always be *least* frequent on isolated stands of low-quality clone 216, and *most* frequent on the high-quality clone 259. Thus, while parasitoid species differ in average PET (Cobbold et al. 2009), this conclusion is independent of the identity of the parasitoid species involved. Moreover, even if PETs for a given parasitoid species differ between aspen clones, outbreak frequencies will only be the same for a few precise combinations of PET dates (see, for example, the arrows denoting PETs necessary for an outbreak frequency of exactly 0.06 across all three clones in Fig. 2). Population fluctuations on isolated genotypes given PET = 37 are shown in Appendix B: Fig. B1.

Observed FTC outbreak frequencies ranged from 0.053 in Vermont to 0.136 in Western Canada (Cobbold et al. 2009); the single-patch outbreak frequencies predicted by this model for the three genotypes (for realistic PETs >25) fall within this range. During FTC outbreaks, the greatest damage to trees is done during the peak of the outbreak when FTC density is highest, but higher median FTC density may also be damaging. In simulations, median FTC density is positively associated with higher peak abundance (Appendix C: Fig. C1); thus, outbreaks are expected to be more frequent but less severe on the higher quality clones, and less frequent but more severe on the lower quality clones.

Because the FTC outbreak frequency on an isolated patch is correlated with the quality of the patch, we will use this single patch result as shorthand when referring to and comparing genotypes in the two-patch models that follow. Specifically, for any genotype combination, we will refer to the lower quality/lower frequency aspen genotype as the "L" genotype and the higher quality/higher frequency genotype as the "H" genotype. Thus, in a 271:259 combination, the medium-quality 271 would be the L genotype, while the high-quality 259 would be the H genotype.

When do outbreaks synchronize in mixed-genotype stands?

Fig. 3 shows an example of the qualitative dynamics of FTC outbreaks in an aspen stand consisting of a patch of genotype 271 (L genotype) coupled to a patch of genotype 259 (H genotype). Outbreak dynamics are shown as a function of patch size ratio (β) and the amount of insect dispersal between patches (m_h and m_p). When there is near-zero dispersal and the L genotype patch is at least as large as the H genotype patch, outbreaks in the two patches occur at different frequencies with different amplitudes (I). At low to moderate dispersal rates, entrainment occurs and outbreaks in the two patches occur with identical frequencies, but peak insect abundance occurs in different years (II). Complete synchrony between patches (III) requires higher dispersal rates and small patch size ratios. The transition from out-of-phase dynamics to in-phase dynamics occurs sequentially across insect species; thus, there are forest compositions that exhibit in-phase parasitoid dynamics, but out-of-phase host dynamics (IV) or in-phase host dynamics, but out-of-phase parasitoid dynamics (V). Finally, when dispersal is high and one patch is much larger than the other, populations of FTC and parasitoids cease to oscillate entirely, exhibiting steady-state dynamics (VI);

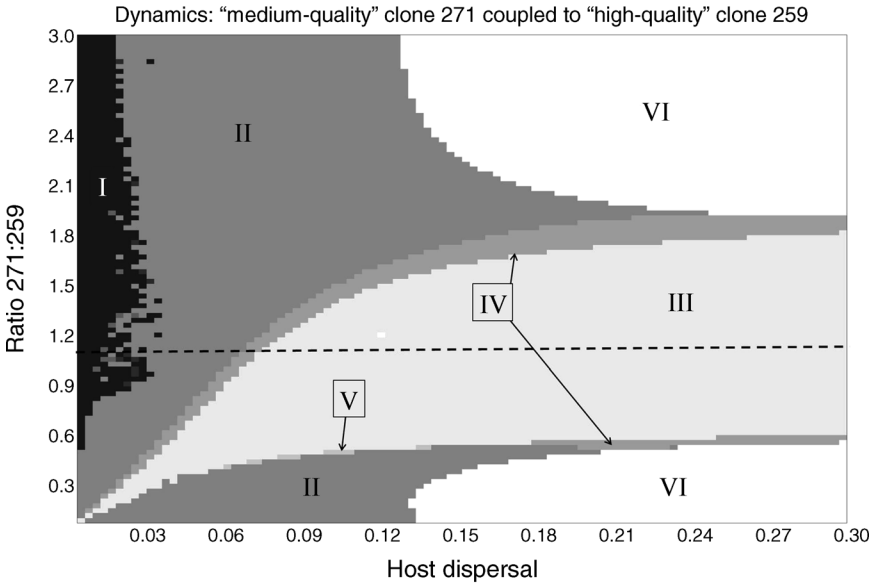

FIG. 3. Synchronicity of host (H) and parasitoid (P) populations for various combinations of patch size ratio (clone 271 : clone 259) and proportion of FTC dispersing. The parasitoid dispersal rate is half the host (FTC) dispersal rate. Host dispersal is the proportion of hosts migrating from one patch to another. Areas are: I, asynchronous oscillations; II, host and parasitoid in both patches exhibit same frequency but different phases; III, synchrony, host and parasitoid; IV, parasitoid synchronized, host out-of-phase; V, host synchronized, parasitoid out of phase; VI, steady state. The dashed line indicates 1:1 patch size ratio.

however, if values of r and α exhibit modest year-to-year stochasticity, these regions are instead asynchronous (Appendix D: Figs. D1–4). Note that Fig. 3 is asymmetric about the 1:1 patch size ratio. When two patches of the same genotype are coupled by dispersal, the graph is symmetric and synchronization occurs more easily at low levels of dispersal (see Appendix D: Fig. D5). The observed asymmetry is the result of heterogeneity in both caterpillar and parasitoid population growth rates. However, results when only α or only r is allowed to vary are very similar (Appendix D: Figs. D6–7), indicating that heterogeneity in the population growth of either species is sufficient for asymmetry.

Qualitative dynamics for all three potential couplings of L to H genotypes were similar (Appendix D: Figs. D8–9), as were dynamics over a wide range of PET values (Appendix D: Figs. D10–11). The ratio of host dispersal to parasitoid dispersal, on the other hand, had a strong effect on phase dynamics. If only hosts disperse, the region in which the frequencies of the two patches are different is larger, and the regions of synchrony or non-oscillatory dynamics are smaller as compared to scenarios where both hosts and parasitoids disperse. If only parasitoids disperse, the shapes of the regions change substantially: For most of parameter space with dispersal >10%, either hosts, parasitoids, or both are synchronized. As the ratio of host dispersal to parasitoid dispersal approaches 2:1, the qualitative dynamics become more similar to those shown in Fig. 3 (Appendix D: Figs. D12–14). This result is consistent with that of Koelle and Vandermeer (2004), who found that increased dispersal could either increase or decrease synchrony, depending on which species in a tri-trophic system dispersed.

How do outbreak characteristics differ in monoclonal vs. mixed-genotype aspen stands?

For the purposes of contrasting outbreak characteristics in single- vs. mixed-genotype forests, two different comparisons are possible: The single-genotype forest can comprise either one large patch or two separate patches with insect dispersal identical to that in the mixed-genotype stand. We will restrict our attention to this latter scenario since it allows a direct comparison between identical forest structures that differ only in their genetic composition.

Are outbreaks more or less frequent in mixed-genotype stands?—Fig. 4a examines how FTC outbreak frequency in a mixed-genotype stand (the medium-quality clone 271 coupled to the high-quality clone 259) differs from outbreak frequency in a single-genotype stand (either 259 or 271). As one might expect, when synchrony is achieved (see Fig. 3), the mixed-genotype stand exhibits a lower outbreak frequency than a stand of the H genotype (259) and a higher outbreak frequency than a stand of the L genotype (271). The outcome is more surprising in systems with patches that are entrained but not perfectly synchronized. In this case, mixed-genotype stands can exhibit outbreak frequencies that are higher or lower than the outbreak frequencies in *either* single-genotype stand. More specifically, when the L genotype patch is larger than the H genotype patch (L:H $>$ 1), the outbreak frequency in the mixed-genotype stand is higher than in either single-genotype stand (black region

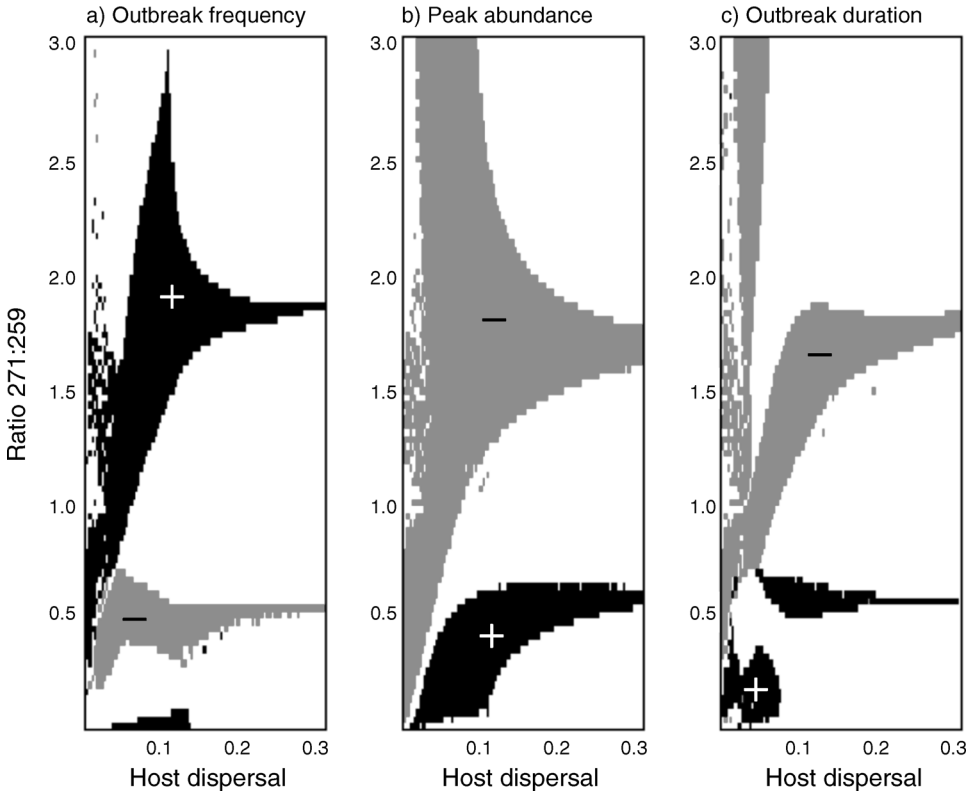

FIG. 4. Difference in (a) FTC frequency, (b) peak abundance, and (c) outbreak duration when a patch of medium-quality clone 271 is coupled to high-quality clone 259 relative to two coupled patches of either clone alone. Host dispersal is the proportion of hosts migrating from one patch to another. Black areas indicate higher values than either clone alone (plus signs), gray areas lower values than either alone (minus signs).

in Fig. 4a). Alternately, when the H genotype patch is larger than the L genotype patch (L:H $<$ 1), the outbreak frequency in the mixed-genotype stand is lower than it is in either single-genotype stand. Similar results were obtained for other L:H combinations.

Outbreak frequencies in mixed genotype stands depend strongly on the relative dispersal abilities of the two insect species. Fig. 4a illustrates a scenario wherein FTCs disperse twice as much as their parasitoids. By contrast, when parasitoid dispersal is higher than FTC dispersal, stands with L:H $<$ 1 can exhibit higher outbreak frequencies than one or both of the single-genotype forests (Appendix D: Fig. D15). Even for these high parasitoid dispersal rates, stands with L:H $>$ 1 continue to exhibit higher outbreak frequencies than stands with L:H $<$ 1, which is somewhat counterintuitive since it is the L genotype (i.e., intrinsically lower outbreak frequency) that dominates.

Are outbreaks more or less severe in mixed-genotype stands?—Fig. 4b and 4c show, respectively, how average peak FTC abundance and outbreak duration differ in a mixed-genotype stand (genotype 271 coupled to 259) as compared to a single-genotype stand. As in Fig. 4a, the black patch shows areas of parameter space in which peak abundance/outbreak duration is higher in the mixed-genotype stand as compared to either single-genotype stand. Likewise, the gray patch shows areas of parameter space in which peak abundance/outbreak duration is lower in the mixed-genotype stand as compared to either single-genotype stand. These regions occur where insect outbreaks exhibit the same frequency but different phases. In keeping with expectation, peak abundance and outbreak duration exhibit an inverse relationship to frequency; thus, regions with higher frequencies have lower peak abundance/outbreak duration, whereas regions with lower frequencies have higher peak abundance/outbreak duration.

DISCUSSION

In this study, we used mathematical modeling to highlight the underappreciated role of plant genotype in governing insect outbreak dynamics. We found that the reported variation in individual FTC performance on different aspen genotypes could drive strikingly different insect dynamics on each (see Fig. 2). This is particularly true when the parasitoids emerge late in the host's development, as small changes in host maturation rate can have large effects on parasitoid mortality due to intra-specific host competition.

Heterogeneity in plant quality and the strength of control by predators and parasitoids is likely to lead to heterogeneity in population dynamics in many herbiv-

orous insects. For instance, differences in gypsy moth outbreak frequency (Haynes et al. 2013) and sawfly gall density across sites (McGeoch and Price 2005) have been linked to differences in predator/parasitoid pressure. Though little is known about how plant quality, mediated through effects on herbivores, affects predators and parasitoids, theoretical studies agree that spatial variation in natural enemies will have important effects on host dynamics (Hassell and May 1988, Nachman 2001). Like tent caterpillars, gypsy moths and other lepidopteran forest pests (Hemming and Lindroth 1995, Hwang and Lindroth 1997, Lindroth et al. 2002) exhibit differences in development on different tree genotypes, though it is not known what role this plays in their population dynamics. Plant genotype has been found to affect population growth rate and other demographic parameters in a variety of plant–insect systems from aphids on strawberries to gall mites on hybrid poplar (Underwood and Rausher 2000, McIntyre and Whitham 2003, Johnson 2008, Underwood 2009), although the significance of this on longer spatial and temporal scales has not been examined.

Even more interesting than the degree of variation in expected outbreak dynamics across plant genotypes is the effect of coupling different clonal patches through insect dispersal. In this study, we show that a forest composed of two different genotypes can exhibit more frequent, less severe insect outbreaks (when the low-quality patch is larger) or less frequent, more severe outbreaks (when the high-quality patch is larger) than would occur in two-patch stands of either genotype alone. This somewhat nonintuitive result occurs when dispersal is low to moderate and patches exhibit entrained but out-of-phase population oscillations. It can be explained as follows: Insect dispersal between out-of-phase patches can result in either amplification or dampening of the host–parasitoid boom–bust cycle. Dispersal that adds insects to "population troughs" or removes them from "population peaks" has a dampening effect, while dispersal that add insects to "population peaks" or removes them from "population troughs" has an amplifying effect. Depending on dispersal between patches, amplifying/dampening mechanisms can be more dominant in mixed-genotype stands compared to single-genotype stands. When this occurs, mixed-genotype stands exhibit lower/higher frequency, and higher/lower outbreak severity than their single-genotype counterparts. This is consistent with a finding by Umbanhower and Hastings (2002) that the number of parasitoids present at low host abundance affects the duration of future host outbreaks. While mixed stands are generally thought to reduce the severity of insect outbreaks, a meta-analysis of over 100 insect herbivores (Jactel and Brockerhoff 2007) found that polyphagous species can exhibit more severe outbreaks in mixed-species stands because they increase their consumption of the less palatable host plant, which buffers them against population collapse; this "spillover effect" is similar to the amplifying effects that the low-quality patch conferred on the high-quality patch in our study.

Simulated outbreak dynamics when a higher quality patch was coupled to a lower quality patch were very similar for all genotypes tested. Thus, despite nonadditive dynamics, one could predict qualitative outbreak dynamics in a mixed-genotype forest based on the relative size of L and H patches and the amount of dispersal between them. FTC outbreaks show less spatial synchrony in the prairie provinces of Canada, where forest patches are highly fragmented, than in Ontario (Cooke et al. 2009). While this corresponds to the lower synchrony we observe in systems with lower dispersal, it does not account for the role of patch quality and its interaction with dispersal, which is the focus of our study. Nevertheless, FTC outbreaks in prairie provinces may be an ideal system for testing hypotheses from our model, particularly if there is substantial variation in plant quality between patches. Other defoliating insects such as jack pine budworm, gypsy moth, and autumnal moth also exhibit geographical variation in synchrony (Bjornstad et al. 2010), and these systems may also offer an opportunity to study the underappreciated interplay between host quality, dispersal ability, and the effectiveness of natural enemies.

As in any simulation study, a few caveats must be mentioned. First, we did not consider the effect of plant genotype on survival of either FTC or parasitoid, as too little data exist to quantify these effects. However, if survival of herbivores differs between plant genotypes, this would have the effect of changing r. This could either reinforce or diminish the effect of differences in pupal mass on population dynamics, depending on whether the herbivore exhibits both low pupal mass and low survival on the same plant genotype. Holton et al. (2003) did find that survival of the generalist parasitoid *Compsilura concinata* was significantly lower in FTC raised on 216, the "low-quality" clone, than on 259, the "high-quality" clone. It is not known whether such an effect might operate in native or more species-specific parasitoid species, but, if so, it would tend to accentuate the negative effect of short host development time on parasitoid survival and would enter the model through α (Eq. 2).

In addition, due to limited data availability, our model was parameterized with data from multiple sites and studies. Ideally, data to parameterize a demographic model should come from the same place and time; however, no study has simultaneously measured the developmental responses of an herbivorous insect to genotypic variation in a food plant, the relationship between development and fecundity, and the role of parasitoids and density-dependent mortality in herbivore population dynamics. Such a study could be conducted to test our conclusions. Another simplification in our model was our assumption that FTC populations occur in just two linked patches, where the spatial relationship between patches is unspecified.

One approach to address this would be to interpret dispersal probability as average dispersal success, relating dispersal to movement and habitat geometry (Fagan and Lutscher 2006). Another complication that is not accounted for in our model is polyphagy. While *Populus tremuloides* is a favorite food plant for northern FTC, many FTC populations utilize more than one plant species, and performance on different tree species varies (Parry and Goyer 2004). Stands containing a greater proportion of the preferred host tree increases defoliation severity in FTC outbreaks, but outbreak duration is reduced when compositional heterogeneity is high (Charbonneau et al. 2012); a similar modeling approach to the one that we introduce in this paper could be used to investigate the effect of different plant species instead of (or in addition to) different genotypes for FTC or other (Jactel and Brockerhoff 2007) polyphagous species. Indeed, in future studies, it would be desirable to develop more spatially explicit models that incorporate a better understanding of how patch geography of multiple host genotypes and species relates to insect dispersal and outbreak characteristics. Finally, little is known about the scale of dispersal in most insect pests and their parasitoids, whether there is a cost to dispersal, or whether insects exhibit preferential dispersal from less favorable to more favorable plant patches. Among forest pests, FTC are considered to have moderate dispersal ability compared to gypsy moth (females non-volant) and spruce budworm (both sexes strong fliers) (Peltonen et al. 2002). The increased severity of local FTC outbreaks (Roland 1993) and the lower levels of synchrony (Cooke et al. 2009) observed in fragmented landscapes, however, suggest that the ability of both insects (and parasitoids in particular) to disperse between widely separated patches may be limited. A more accurate understanding of dispersal behavior in both FTCs and their parasitoids would certainly improve the predictive power of the model.

The mechanisms responsible for plant genotype influence on insect dynamics are not restricted to the aspen–FTC–parasitoid system. Like aspen, many other plants exhibit genotypic variation in the levels of defensive compounds (Bailey et al. 2006, Vannette and Hunter 2011) and herbivore performance (Hemming and Lindroth 1995, Hwang and Lindroth 1997, Cronin and Abrahamson 1999, Underwood and Rausher 2000, Lindroth et al. 2002, Holton et al. 2003, Kopper and Lindroth 2003, Johnson 2008). Effects of host plant genotype on herbivore dynamics similar to those simulated here are expected whenever birth or death rates are substantially different between plant genotypes and the scale of genetic heterogeneity is large relative to insect dispersal ability. It should, however, be noted that individual performance measures (such as pupal mass) might not be good predictors of demographically important processes in all species. Whether differences in demographic rates on different genotypes leads to "intermediate" landscape-level dynamics, such as observed here in the case of high dispersal and similar patch size, or to more complex dynamics, such as observed in the case of low-to-moderate dispersal and unequal patch size, will depend on the dispersal ability of the insect in question relative to the size of genotypic patches. As large patches of genetically similar plants frequently occur in agricultural or silvicultural systems (Karnosky 1981, Andow 1983, Zhu et al. 2000, Park 2002), these may be other instances of systems with relatively dramatic genotypic effects. This has interesting implications, since a better understanding of the effect of plant genotype and landscape connectivity on insect population dynamics in managed landscapes could help to minimize the most damaging aspects of herbivore population dynamics, whether that be outbreak frequency or insect abundance. The patchy distribution of plant clones in wetlands and grasslands (Eriksson 1989, Barrett et al. 1993, Amsberry et al. 2000, Pennings and Callaway 2000) could also affect insect dynamics in these ecosystems. While much remains to be learned, we hope that our study draws attention to the effects plant genotype may have on herbivore population dynamics.

Acknowledgments

We thank Richard Lindroth for sharing the original FTC performance data. This work was conducted while E. V. Moran and S. Bewick were postdoctoral fellows at the National Institute for Mathematical and Biological Synthesis (NIMBioS); C. A. Cobbold assisted by attendance as a short-term visitor at NIMBioS. NIMBioS is an institute sponsored by NSF, the U.S. Department of Homeland Security, and the USDA through NSF award number EF-0832858, with additional support from the University of Tennessee.

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Supplemental Material

Appendix A

A description of Aspen FACE forest tent caterpillars (FTC) data (*Ecological Archives* E094-258-A1).

Appendix B

Further details on parameter estimation (*Ecological Archives* E094-258-A2).

Appendix C

The relationship between median FTC density and peak population size (*Ecological Archives* E094-258-A3).

Appendix D

Figures depicting the effects on population dynamics of stochasticity in α and r, linking two patches of the same genotype, and the variation in α or r alone; phase diagrams for the other genotype combinations; the effect of changing PET or parasitoid : host dispersal ratios; and a graph showing oscillatory dynamics when parasitoid dispersal is higher than host dispersal (*Ecological Archives* E094-258-A4).