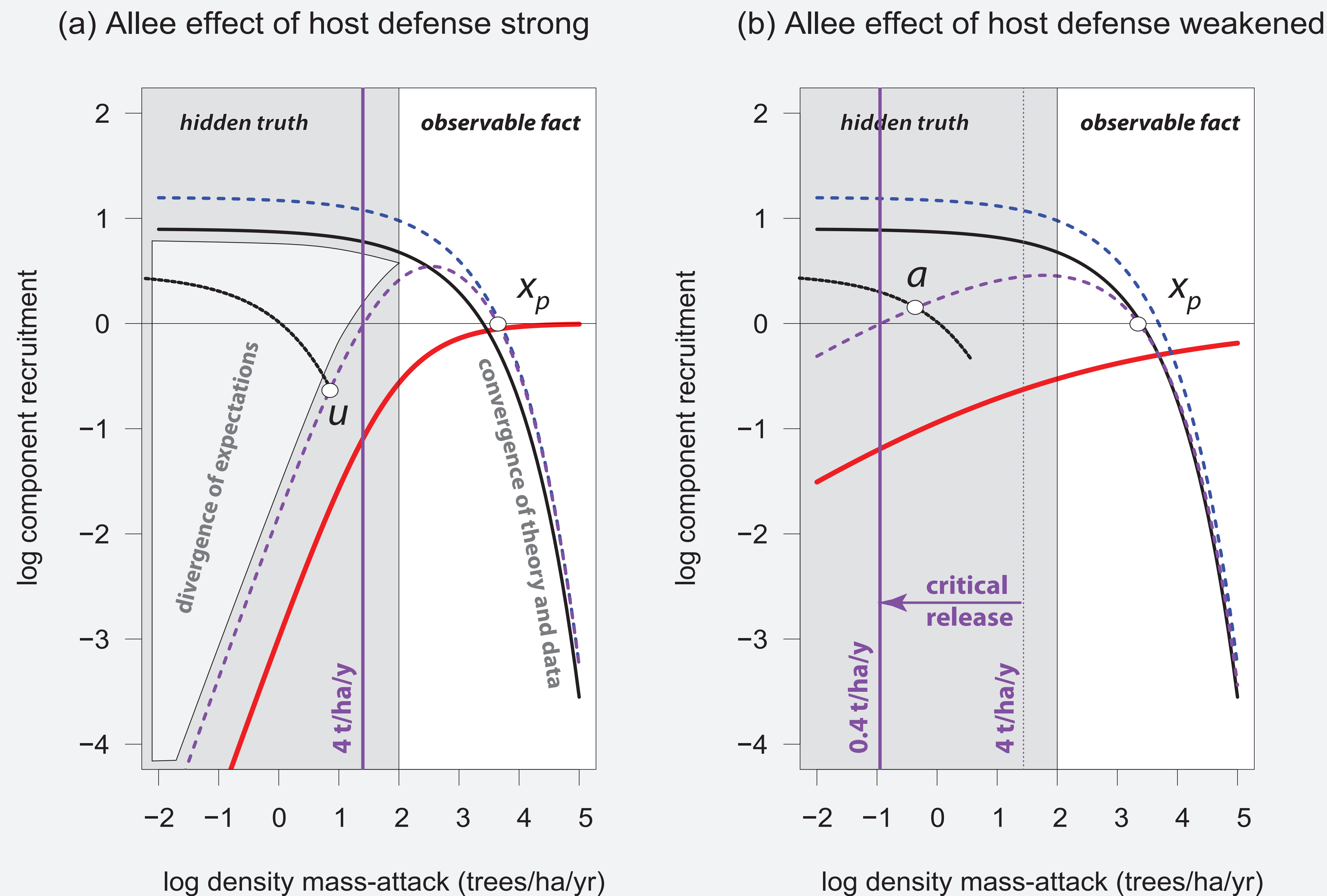




# The hidden role of **host defense relaxation** in MPB release: a lesson in real-world, **low-density nonlinear dynamics**

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## METHODS

Data from Boone et al. (2011) were fit using logit-Hill functions. Data from MacQuarrie and Cooke (2011) were fit using negative exponentials. The net recruitment curve (purple) was computed as the product of the component Allee effect (red) and the inferred recruitment component (blue). The endemic recruitment curve is assumed, but results are qualitatively insensitive to its shape.

data	
<span style="color: red;">—</span>	Boone et al. (2011) component Allee effect
<span style="color: black;">—</span>	MacQuarrie & Cooke (2011) recruitment curve
theory	
<span style="color: blue;">- - -</span>	inferred component recruitment
<span style="color: purple;">- - -</span>	computed net recruitment curve
<span style="color: purple;">—</span>	release threshold
<span style="color: black;">- - -</span>	assumed recruitment in endemic niche

## RESULTS

Fig. 1. The dynamics of relaxation release are not observable in operational ADS (aka "red-top") data. The right-hand side of the graphs contrast that which is observable in operational data, versus the left-hand-side of the graphs (shaded), where "careful observation" is required. In panel (a) host defenses are strong, leading to heavy pitch-out of adult beetles and heavy resinosis of eggs and young larvae (red curve). As attack densities rise, the component effect of aggregative co-operation leads to higher component recruitment. As attack densities rise further, beyond peak, overall recruitment (dashed purple) is dominated by competitive effects that arise in the late larval recruitment component (dashed blue). In the absence of mass-immigration crossing the 4 trees/ha/y threshold, no outbreak is possible because the epidemic niche (purple) is unavailable ("u") to MPB existing in the endemic niche (dashed black). In panel (b), one year later, host defenses have been compromised by drought stress, the component Allee effect of host defenses weakens, recruitment rises, and the critical threshold for outbreak drops from 4 trees/ha/y to 0.4 trees/ha/year. Now, populations in the endemic niche that were formerly incapable of mass-attacking at a rate of one tree per hectare per year may explode to a new equilibrium level, "xp", as the epidemic niche is now effectively available ("a"). The process of recruitment curve intersection point "u" moving from position  $R < 0$  to position "a", where  $R > 0$ , is called a "saddle-node bifurcation" and is the formal mathematical definition of "outbreak".

## DISCUSSION

### "Careful" observation:

- observation of endemic populations ( $< 1$  tree/ha/y), several years prior to eruption
- ground-based tree population census in large plots, tens of hectares in size
- population growth absent any mass-immigration
- observation during a long enough interval that environmental conditions and host defenses change considerably
- these necessary conditions are extremely rare in field circumstances, and do not occur in operational circumstances

### The hidden enemy:

- relaxation of host defenses triggering outbreak has been modelled by Berryman (1975, 1979, 1986, 1999)
- component Allee effect of host defenses has been shown in experiments by Raffa (1983)
- eruption in real-world populations occurs at densities well below operational detection thresholds
- these effects have never been modelled using well-calibrated, field-validated component recruitment curves

### Critical uncertainty:

- Is the role of drought in triggering MPB outbreak in BC understated?
- If boreal jack pine come with "pre-relaxed" defenses (as in panel b), eruptive spread is far more likely