Pulse and Press Disturbances Have Different Effects on Transient Community Dynamics

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Abstract: Disturbances are important determinants of diversity, and the combination of their aspects (e.g., disturbance intensity, frequency) can result in complex diversity patterns. Here, we leverage an important approach to classifying disturbances in terms of temporal span to understand the implications for species coexistence: pulse disturbances are acute and discrete events, while press disturbances occur continuously through time. We incorporate the resultant mortality rates into a common framework involving disturbance frequency and intensity. Press disturbances can be encoded into models in two distinct ways, and we show that the appropriateness of each depends on the type of data available. Using this framework, we compare the effects of pulse versus press disturbance on both asymptotic and transient dynamics of a two-species Lotka-Volterra competition model to understand how they engage with equalizing mechanisms of coexistence. We show that press and pulse disturbances differ in transient behavior, though their asymptotic diversity patterns are similar. Our work shows that these differences depend on how the underlying disturbance aspects interact and that the two ways of characterizing press disturbances can lead to contrasting interpretations of disturbance-diversity relationships. Our work demonstrates how theoretical modeling can strategically guide and help the interpretation of empirical work.

Keywords: press disturbance, pulse disturbance, mortality rate, transient dynamics, equalizing mechanism.

Introduction

Recurrent mortality-inducing disturbance events, such as fires and floods, are ubiquitous and important determinants of ecological community structure (Levin and Paine 1974; Connell 1978; Huston 1979; Sousa 1984). Through mortality of competitors, disturbance alters the amount of competition experienced by the survivors and thus alters competitive outcomes. Ecologists have been particularly interested in the effects of disturbance on the diversity of the resulting competitive community. A body of theoretical (Chesson and Huntly 1997; Kondoh 2001; Roxburgh et al. 2004; Miller et al. 2011) and empirical work (Buckling et al. 2000; Mackey and Currie 2001; Walker 2011) spanning a wide range of taxa has analyzed the effects of disturbance on diversity, but the general form of the relationship has remained elusive (Mackey and Currie 2001). Historically, different aspects of disturbance (e.g., frequency, intensity, timing, duration, extent) were thought to have similar effects on diversity (Connell 1978). However, recent work (Roxburgh et al. 2004; Shea et al. 2004) has shown that a major challenge in understanding the disturbance-diversity relationship lies in the difficulty of comparing various types and aspects of disturbances driving different ecological systems (e.g., timing of pasture mowing, intensity and frequency of hurricanes, duration of droughts, extent of forest-defoliating insect outbreaks). Disturbance can be described by a combination of their aspects, and a systematic understanding of the effects of each aspect on diversity is needed (Shea et al. 2004).

Recent theoretical work has shown that different disturbance aspects interact in complex ways to generate community structure (Miller et al. 2011, 2012a). In a simple competition model, Miller et al. (2011) showed that the diversity pattern generated as disturbance frequency changes depends crucially on its intensity, and vice versa, and the patterns generated across frequency may differ from those generated across intensity. Importantly, these disturbance-diversity relationships mirror the wide range

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of patterns commonly found in empirical systems (Mackey and Currie 2001) and predict the patterns found in experimental microcosms (Hall et al. 2012). Taken together, it is clear that the disturbance-diversity relationship depends on the aspects studied in each system. Consequently, different combinations of disturbance aspects may result in similar overall destruction of biomass, but their effects on competition and the resulting community may diverge (Miller et al. 2012a). Hereafter, we call these specific combinations of quantified aspects of disturbance “regimes,” for example, high intensity but low frequency versus low intensity but high frequency.

One ecologically important and common approach to classifying disturbance regimes is to partition them into events that have discrete and acute effects and events whose effects are diffuse and sustained. These regimes are commonly known as pulse and press disturbances, respectively (Bender et al. 1984), though the medical and stress literature refers to the terms “acute” and “chronic” (McCormick et al. 2015). Pulse disturbances are events with discrete and relatively short mortality events, whereas press disturbances are events with continuous disturbance with mortality occurring in a sustained manner over long durations (Jentsch and White 2019; Miller et al. 2021; fig. 1). Previous work has studied the effects of pulse (Buckling et al. 2000; Yang 2004; Yang et al. 2008; Hillebrand and Kunze 2020) and press (Fussmann et al. 2000; Angeler and Moreno 2007; Tonkin and Death 2012; Van Diggelen and Montagna 2016; Eckert et al. 2019; Claar et al. 2020) regimes on diversity. However, it is unclear a priori how to equitably compare the effects of these two regime types in a way that effectively isolates the variation in aspects of disturbance such as duration, frequency, and intensity.

For example, consider an annual census of a species at a field site where an unobserved disturbance kills a proportion of its population (fig. 1). The intercensus population dynamics would differ if the disturbance regime was a press (e.g., a drought), a series of small pulses (e.g., fires), or a single large pulse (e.g., a volcanic explosion), even if the three disturbance scenarios result in the same population size at the next census (Butler 1989; Agur et al. 1993; Navarrete 1996). In a complex community, each of these scenarios may also result in different species interactions, thus further altering community composition: the intensity of resource competition drops suddenly under a single large pulse disturbance, whereas it may gradually decrease under a steady press disturbance. While the importance of transient trajectories has been highlighted in both theoretical and empirical systems (Hastings 2001; LaBar et al. 2013; Kotil and Vetsigian 2018; Amor et al. 2020), a systematic theoretical analysis of the transient effects of pulse versus press on diversity has not been previously conducted. Using a model of competitive community dynamics, we explore the transient effects of pulse disturbances on populations by comparing them with models of press disturbances with equivalent overall disturbance-induced mortality and show that the press/pulse distinction strongly affects the transient dynamics of a competitive community.

Disturbance can engage with both stabilizing and equalizing mechanisms of species coexistence (Chesson and Huntly 1997; Chesson 2000; Miller et al. 2012a). Stabilizing mechanisms facilitate coexistence by strengthening negative density-dependent population growth so that a species can rebound from low densities. For example, disturbances may lead to reduced competition for poorly surviving species (e.g., storage effect). In contrast, equalizing mechanisms delay competitive exclusion by reducing fitness difference between species. For example, disturbances may affect the dominant species more than the others, resulting in a smaller overall fitness difference between the species. Much of the previous work on the effect of disturbance has focused on its role as a stabilizing mechanism and how it affects the long-term steady-state competitive outcome; its role as an equalizing mechanism has been somewhat neglected (but see Huston 1979, 2014). Equalizing mechanisms may be especially important in pulse regimes because pulse events push a community to transiently diverge away from its dynamical trajectory (Holt 2008). Equalizing mechanisms are not necessary or sufficient for stable coexistence, but they can be critically important in

Figure 1: Intercensus population dynamics vary greatly among disturbance regimes. Consider an annual census of a hypothetical population taken at two time points (circles). Population size may decrease between the two time points as a result of a press disturbance (solid magenta line), several low-mortality pulse events (dotted line), or a single large-mortality pulse event (dashed line). All three disturbance scenarios have the same population sizes at each census, but their unobserved intercensus population dynamics differ greatly.

\[
\begin{align*}
N_0 & \rightarrow N_1 \\
\text{Press} & \quad \text{Small pulses} & \quad \text{Large pulse}
\end{align*}
\]
determining community composition because they may reduce the strength of stabilizing mechanisms needed to produce stable coexistence. By delaying time to competitive exclusion, equalizing mechanisms can essentially buy time for extant stabilizing mechanisms to act (e.g., seed banks) or allow new ones to form (e.g., through changes to environmental variation, niche differentiation as a result of character displacement). We therefore focus here on equalizing mechanisms by employing a competition model where the competition terms are linear, which formally prevents disturbance from acting as a stabilizing mechanism; fluctuation in dominance due to disturbance cancels out in the long run, and the species with the highest average dominance eventually outcompetes the others (Chesson and Huntly 1997; Fox 2013).

In practice, representing empirical data in appropriate theoretical models to understand how mortality affects the dynamics of a focal community is not straightforward, with potential pitfalls for interpretation (Sheil et al. 1995). A common approach to understanding the effects of disturbance is to consider the overall mortality rate that a population experiences under a certain disturbance regime. However, the manner in which the mortality rate is structured and parameterized may depend on the type of disturbance data gathered. For example, data collected on time since the last fire event and the percent of vegetation burned by fire (information on the frequency and intensity of disturbance, respectively) give different information from data on population size at each census time. These two types of data (measurements on aspects of disturbance and measurements on population size) may lead to vastly different conceptions of the disturbance process. Specifically, disturbance-induced mortality rates calculated from the former data type may focus on the average return time of the disturbance event, whereas the rates derived from the latter data type result from getting the exact population size at each time point. We derive two different methods of defining mortality rate for press disturbances using these data types and show how the two methods differ with respect to their effect on mortality. Using this framework, we compare the differential effects of pulse versus press disturbances of different frequency and intensity on competitive outcomes. We also briefly discuss the effects of different parameterizations on projected community dynamics and the implications for inference from data on disturbed systems.

Methods

Baseline Competitive Lotka-Volterra Model

We analyzed the effects of disturbance on a community of competing species by using a scaled competitive Lotka-Volterra model (Verhulst 1838; Lotka 1925):

\[
\frac{dp_i}{dt} = p_i(1 - p_i - \alpha_{ij}p_j), \\
\frac{dp_j}{dt} = \beta p_j(1 - p_j - \alpha_{ij}p_i),
\]

(1)

where \(p_i\) is the population density of species \(i\), \(\alpha_{ij}\) is the competitive coefficient of species \(j\) on species \(i\), and \(\beta\) is the growth rate of species \(2\) relative to species \(1\). In this model, time is scaled by the growth rate of species \(1\) so that the time unit of the simulation is the timescale associated with the exponential growth rate of species \(1\) \((1/r_1)\), where \(r_1\) is the maximum reproductive growth rate of species \(1\); see sec. S1 in the supplemental PDF). We layered a disturbance model on equations (1) as described in “Pulse and Press Disturbance.” The linear competition terms in equations (1) prevent any disturbance regime from engaging with fluctuation-dependent stabilizing mechanisms (Chesson and Huntly 1997; Fox 2013), allowing us to focus on the equalizing effects of disturbance. We chose parameters so that the system is bistable to eliminate the possibility of stable coexistence.

Pulse and Press Disturbance

To compare the effects of pulse and press disturbances on community dynamics, we modeled the two disturbance regimes as follows. For pulse disturbance, we generated \(x\) disturbance events at regular intervals over a time span \(T\) so that the disturbance frequency \(f = x/T\). Each disturbance event kills fraction \(I\) of individuals (for details and model variants, including models with stochastic rather than regular intervals, see sec. S2 in the supplemental PDF). For press disturbances, we model disturbance as a continuous additional mortality rate, such that

\[
\frac{dp_i}{dt} = p_i(1 - p_i - \alpha_{ij}p_j) - \mu p_i, \\
\frac{dp_j}{dt} = \beta p_j(1 - p_j - \alpha_{ij}p_i) - \mu p_j,
\]

(2)

where \(\mu\) is the additional mortality rate due to the press disturbance.

There are a few choices available for how to define \(\mu\) so that the resulting press disturbance provides a death rate in some sense analogous to a pulse disturbance with a frequency \(f\). A common definition of \(\mu\) is \(\mu_{\text{adi}} = f I\). This intuitive approach is appealing: the idea is to create an instantaneous (continuous) mortality that kills the same number of individuals as pulse events, with intensity \(I\) recurring, on average, every \(1/f = T/x\) time units. Importantly, this formulation assumes that the effects of frequency and intensity of disturbance regimes are symmetrical and, therefore, that the disturbance aspects are interchangeable: a small change in frequency affects the population and
community outcomes exactly as the same small change in intensity would. This \( \mu_{\text{rate}} \) may be natural to calculate from data on measurements of disturbance aspects, for example, data collected on time since the last fire outbreak and the percent of field vegetation burned by fire. However, this formulation always overestimates the final population size compared with the pulse model for any \( f, I \), and intercensus period \( T \) when disturbance is the only demographic process driving the population dynamics (i.e., without competition, reproduction, or natural mortality; supplemental PDF, sec. S3; fig. S3). Because this model focuses on return time as a rate, hereafter we call press disturbance using \( \mu_{\text{rate}} \) a “rate press” model.

Alternatively, we also analyzed the choice of defining \( \mu \) in a way that is designed to generate the same number of deaths as the pulse disturbance, if the mortality from disturbance is the only demographic process driving the population dynamics. The result of this requirement is \( \mu_{\text{endpoint}} = -f \cdot \log(1 - I) \) (see sec. S3 in the supplemental PDF). Although calculating \( \mu_{\text{endpoint}} \) requires strict assumptions that no other demographic processes operate, it may be more natural and practical to calculate \( \mu_{\text{endpoint}} \) than \( \mu_{\text{rate}} \) from data on population size. Note that without data on frequency and intensity of disturbance, \( \mu_{\text{endpoint}} \) is a phenomenological parameter backcalculated by fitting population size to a model. Because this model focuses on getting the exact population size at a census time (endpoint of population dynamic), hereafter we call press disturbance using \( \mu_{\text{endpoint}} \) an “endpoint press” model.

The two choices for \( \mu \) have different implications for population dynamics as well as for empirical data collection and forecasting. To analyze the models, we compared a suite of pulse models with disturbance parameters \( (f, I) \) with the equivalent rate press model and with the equivalent endpoint press model.

**Simulation**

We numerically solved the Lotka-Volterra model with either press or pulse disturbances using the R package deSolve (Soetaert et al. 2010). We initialized each simulation with \( p_1 = p_2 = 1 \) and used the following parameters: \( \beta = 2 \), \( \alpha_{12} = 1 \), and \( \alpha_{21} = 1.01 \). Under these parameters, species 1 is more competitive than species 2 (\( \alpha_{21} \geq \alpha_{12} \)) but species 2 grows faster than species 1 (\( \beta > 1 \)). Note that without disturbance, species 1 excludes species 2 under this parameter set and initial condition but the system is bistable so species 2 can exclude species 1 with sufficient disturbance. After running each simulation for 3,000 time units (long enough for one species to out-compete the other), we recorded the population sizes averaged across the last 100 time units of the simulation (final population sizes) to average out the fluctuations in the population sizes caused by the disturbances. We additionally recorded the time until one of the species falls and stays below a population threshold of \( 10^{-3} \) (co-occurrence time) to understand the transient dynamics of the competing pair. We performed simulations across the full frequency-intensity parameter space (i.e., from always to never disturbed, with no to complete mortality), sampling values from 0.01 to 1 on a log scale, so that frequencies are sampled equitably across the whole (0, 1) range. To understand the differential effects of pulse and press disturbances, we then calculated the difference in final population sizes and co-occurrence time between all variants of the two disturbance types across the entire parameter space. We plotted these values across the parameter space to visually understand how these values change over different disturbance regimes. For the final population sizes, we further renormalized the subset \( S \) of the parameter space \( (I \geq 0.1, f \geq 0.1; \text{dashed enclosure in fig. 2b}) \) to highlight the variation in this region. Specifically, we recalculated the \( i^{th} \) data point \( x_i \) in \( S \) as \( x_i / \max_{x_j \in S}[x_j] \), where the maximum is taken over the subset. All computations were performed in R version 3.4.0 (R Development Core Team 2017).

**Results**

We modeled press mortality rate \( \mu \) with two separate methods to enable controlled interpretations of the differences generated by different press and pulse regimes. For a given pulse regime with disturbance frequency \( f \) and intensity \( I \), we modeled press regime \( \mu \) as \( \mu_{\text{rate}} = fI \) or as \( \mu_{\text{endpoint}} = -f \cdot \log(1 - I) \). Even with the simplest baseline population dynamics model, both press models diverged substantially from the pulse models over time (figs. S3, S4). We investigated how this transient difference in population dynamics between press and pulse regimes leads to transient but ecologically important differences in community dynamics.

Pulse and press disturbance models had very similar asymptotic outcomes, as measured by their final population sizes. In all cases, species 1 (the more competitive species) outcompeted species 2 (the faster-growing species) when disturbance frequency and/or intensity was low, but the reverse was true when disturbance frequency and/or intensity was high (figs. 2, S5). The transition in competitive outcome occurred over a narrow boundary running diagonally in parameter space (hereafter, we call this subset of parameter space where the competitive outcome flips the “transition boundary”); note that the axes of the parameter space are on a log scale.

The differences in final population sizes between pulse and endpoint press models were minimal, with only a
Δ Final population size of species 1:
Pulse – Endpoint press

| Frequency |
|----------|
| 1.00     |
| 0.50     |
| 0.10     |
| 0.05     |
| 0.01     |

Pulse > Endpoint press
Pulse < Endpoint press

Δ Final population size of species 2:
Pulse – Endpoint press

| Frequency |
|----------|
| 1.00     |
| 0.50     |
| 0.10     |
| 0.05     |
| 0.01     |

Pulse > Endpoint press
Pulse < Endpoint press

Δ Final population size of species 1:
Pulse – Rate press

| Frequency |
|----------|
| 1.00     |
| 0.50     |
| 0.10     |
| 0.05     |
| 0.01     |

Pulse > Rate press
Pulse < Rate press

Δ Final population size of species 2:
Pulse – Rate press

| Frequency |
|----------|
| 1.00     |
| 0.50     |
| 0.10     |
| 0.05     |
| 0.01     |

Pulse > Rate press
Pulse < Rate press

Figure 2: Difference in final population sizes between pulse and press disturbances. Disturbance-induced death rate in the press model was defined as either $\mu_{\text{press}} = -f \log(1 - l) (a, b)$ or $\mu_{\text{rate}} = f I (c, d)$. Each point in the parameter space is the difference in final population sizes for species 1 ($a, c$) or species 2 ($b, d$), that is, final population size in the pulse model minus the final population size in the equivalent press model. Points in the parameter space with positive values are red, and points with negative values are blue (color intensity increasing with the magnitude). The pulse model had a larger population size for species 1 but a smaller population size for species 2 compared with endpoint press around the transition boundary, whereas the opposite was true when compared with the rate press model. Note that the color intensity in the subset parameter space $I \geq 0.1, f \geq 0.1$ (dashed enclosure in b) is renormalized to highlight the variation in values in this region. For full visualization of each region, see figures S5–S7. The parameters used in these simulations are $\beta = 2$, $\alpha_{12} = 1$, and $\alpha_{21} = 1.01$. Each simulation started with $p_i = p_l = 1$ and ran for 3,000 time units.
small difference in where the transition boundary occurred (fig. 2a, 2b): the increase in the final population size in species 1 under pulse disturbance at the transition boundary accompanied a decrease in the final population size in species 2. The transition boundary—and the combinations of intensity and frequency of disturbance regime that flips the competitive outcome—therefore shifted slightly toward the lower frequencies and intensities region of the parameter space under endpoint press disturbances compared with pulse disturbances. Also note that the final population size for species 2 was higher in pulsed disturbance regimes than in endpoint press disturbance regimes in the high frequencies and intensities region of the parameter space (fig. 2b, dashed enclosure), but the final population size for species 1 did not change between the two regimes in the same region of the parameter space (fig. 2a). This implies that while species 2 outcompeted species 1 in that region of the parameter space, species 2 maintained a larger size under pulse dynamics because of the relaxation time in between disturbance events. The difference in final population sizes between pulse and rate press models was larger, with more pronounced discordance near the transition boundary (fig. 2c, 2d).

The transient dynamics give us a better understanding of the differences caused by press versus pulse disturbance dynamics. As expected, co-occurrence times were longer (and competitive exclusion was slower) around the transition boundary compared with other regions of the parameter space (fig. 3). Co-occurrence times were generally shorter for the communities under high-frequency and high-intensity regimes compared with those under low-frequency and low-intensity regimes. This implies that as intensity or frequency of disturbance increased, it promoted the persistence of species 2 and the extinction of species 1. When the data from figure 3 were plotted against the press mortality rate \( \mu \) (fig. 4), we observed that both press and pulse regimes can significantly delay competitive exclusion, even up to the end of the simulation period (without disturbance, the species pair will co-occur for \( \approx 450 \) time units). We also observed that co-occurrence times first increase with increasing \( \mu \) but then decrease sharply after a threshold value. However, while the co-occurrence times across \( \mu \) were similar for pulse and endpoint press regimes, they diverged substantially between pulse and rate press regimes.

To further analyze how co-occurrence times diverge between the pulse and each of the press models, we calculated the difference in co-occurrence times across the frequency-intensity parameter space (fig. 5). As in the pattern in final population size (fig. 2), we observed differences in co-occurrence time near the transition boundary due to the fact that the transition boundaries between pulse and press regimes do not exactly coincide. Unlike the pattern in final population size, however, we observed a greater difference in co-occurrence time in the parameter space where disturbance frequency is low and intensity is high but not where frequency is high and intensity is low, perhaps because high-frequency, low-intensity pulse regimes behave similarly to press disturbance regimes. This pattern is consistent across both differences in co-occurrence time between pulse and endpoint press disturbances as well as between pulse and rate press disturbances. The two comparisons are remarkably different, however, when we analyze the sign of the difference in co-occurrence time. Pulse disturbance generally shortened co-occurrence times compared with endpoint press disturbances on the lower frequencies and intensities side of the transition boundary but lengthened co-occurrence time on the higher frequencies and intensities side of the transition boundary (fig. 5a), whereas pulse disturbance generally lengthened co-occurrence time compared with endpoint press on the lower frequencies and intensities side of the transition boundary but shortened co-occurrence time on the higher frequencies and intensities side of the transition boundary (fig. 5b). The opposite patterns in sign we see around the transition boundary indicate that the choice of \( \mu \) can profoundly change our interpretation of the effects of press versus pulse disturbance on populations and the community. We further investigated these opposite patterns around the transition boundary by plotting the model results against the press mortality rate \( \mu \) (fig. 6). In both endpoint press and rate press disturbance regimes, the difference in co-occurrence times was small at low and high \( \mu \) but large at intermediate rates. Within this intermediate range, pulse disturbance regimes shortened co-occurrence times compared with endpoint press disturbance regimes when the \( \mu \) is low but lengthened them when \( \mu \) is high (fig. 6a). On the other hand, pulse disturbances lengthened co-occurrence time compared with rate press disturbances when \( \mu \) is low but shortened it when \( \mu \) is high (fig. 6b). The difference in co-occurrence time reaches a magnitude of 1,000 time units when compared with endpoint press disturbances and 2,000 time units when compared with rate press. This is a large difference in co-occurrence time and therefore large transient divergence in community dynamics between pulse and press disturbances, given that co-occurrence occurs for only \( \approx 450 \) time units under no disturbance.

**Discussion**

Disturbances affect all components of ecological systems, and ecological systems have always been perturbed. Press and pulse disturbances have long been used as important research tools in both field and laboratory experiments (Bender et al. 1984; Yang 2004; Garrison et al. 2012; Seifarth et al. 2021) as well as providing a lens through which
to understand and interpret behavior of ecological communities (Levin and Paine 1974; Connell 1978; Huston 1979; Sousa 1984). Many researchers have shown that disturbance is a key driver of diversity, but the multifaceted nature of disturbance proves challenging to our ability to understand the exact mechanisms underlying coexistence and competitive exclusion. Disturbances are commonly categorized as press or pulse, yet how these two regime types and their effects fundamentally differ has been unclear. By focusing on the overall mortality rate, we build

Figure 3: Co-occurrence time of competing species pair under pulse (a) and press (b, c) disturbances. Disturbance-induced death rate in the press model was defined as either $\mu_{\text{death}} = -f \log(1 - I)$ (b) or $\mu_{\text{rate}} = fI$ (c). The color intensity of each point in the parameter space is darker with increasing co-occurrence time (defined as the time until one of the species dips and stays below the population size threshold of $10^{-2}$). While there are small differences between these plots, their key shared feature is the diagonal transition boundary that shows the region of the parameter space where disturbances delay competitive exclusions. The average co-occurrence times (averaged across the entire parameter space) and their standard deviations are $504.0 \pm 377.1$ (a), $504.6 \pm 373.5$ (b), and $527.4 \pm 366.1$ (c) time units.
Figure 4: Co-occurrence time under pulse and press regimes across $\mu$. The same data from figure 3 on co-occurrence time under pulse (black) and press (magenta) regimes are plotted against the press mortality rate, defined as either $\mu_{\text{endpoint}} = -f \log(1 - I)$ (a) or $\mu_{\text{rate}} = fI$ (b). The dotted horizontal line indicates the maximum simulation time.

Figure 5: Difference in co-occurrence time between pulse and press disturbances. Disturbance-induced death rate in the press model was defined as either $\mu_{\text{endpoint}} = -f \log(1 - I)$ (a) or $\mu_{\text{rate}} = fI$ (b). Each point in the parameter space is the difference in co-occurrence times, that is, co-occurrence time in the pulse model minus the co-occurrence time in the equivalent press model. Points in the parameter space with positive values are red, and points with negative values are blue (color intensity increasing with the magnitude).
a framework to reduce both regimes to the common cur-
rencies of disturbance intensity and frequency.
We consider two different ways of characterizing press
disturbances so that both regimes lead to the same mor-
tality rate. Press regimes with \( m \) endpoint focus on population
sizes at a census by forcing population sizes to be equal
between press and pulse regimes. Press regimes with \( m \)
rate focus on the average return time of disturbance events.
Both press models transiently diverge from the analogous
pulse model. While press regimes with \( m \) endpoint sometimes
showed greater divergence than regimes with \( m \) rate in a
single-species population dynamics model (figs. S3, S4), regimes with \( m \) rate always overestimate population size
when disturbance is the only demographic process driv-
ing population dynamics.

The difference between the two methods is not only
quantitative but also qualitative and important: analyses
performed using \( m \) rate show that the effects of disturbance
intensity and frequency on co-occurrence time are oppo-
site of those obtained using \( m \) endpoint: pulse disturbances
lengthened co-occurrence time compared with press dis-
turbance when \( m \) rate is low but shortened it when \( m \) rate is
high. A contrasting effect of pulse versus press disturbances
on key community properties (such as co-occurrence time)
therefore crucially depends on the underlying character-
ization of the disturbance process and on the assumptions
used in the model. Given that these characterizations are
in turn approached on an ad hoc basis, depending on the
way that data are collected or parameterization is moti-
vated, this constitutes a significant impediment to the de-
velopment of a deeper theoretical understanding of dis-
turbance and its ecological effects.

Pulse and press regimes generally show similar effects
of disturbance on long-term diversity measures but dif-
fer in their effects on transient measures, such as co-
occurrence time. Transient community states may be
especially important for management and for evolution.
In our model, the two competing species co-occur for
\( \approx 450 \) time units without disturbance and can co-occur for
2,000 time units longer with disturbance; that is, with distur-
bance, co-occurrence times can be increased to over four
times as many generations compared with the case with-
out disturbance. Disturbance can therefore sig-
ficantly delay the time to extinction, during which time manage-
ment, environmental change, and/or evolution can poten-
tially rescue an endangered species from extinction. Tran-
sient dynamics are especially important under pulse
regimes, where the system relaxes after each disturbance
event. In our models, the co-occurrence times arising in
pulse regimes differ the most from those arising in press
regimes the most when disturbance frequency is low but
intensity is high, that is, rare but devastating disturbances
such as volcanic explosions or hurricanes. After such a pulse
event, the population may take a while to return to its

Figure 6: Difference in co-occurrence time across \( \mu \). The same data from figure 5 (co-occurrence time in the pulse model minus co-
occurrence time in the equivalent press model) are plotted against the press mortality rate, defined as either \( \mu_{\text{endpoint}} = -f \log(1 - I) \) (a) or
\( \mu_{\text{rate}} = f I \) (b). The cyan data points were collected from disturbance regimes with \( I \geq 0.2 \) and \( f \leq 0.05 \) (i.e., bottom right corner of the
parameter space in fig. 5a, 5b), roughly corresponding to a block of parameter space with large differences between the pulse and press mod-
els. Note that the cyan data points show opposite patterns in the sign between \( a \) and \( b \).
original trajectory and therefore transiently diverge from the equivalent press regime. This transient difference between press and pulse can result in further differences in co-occurrence time, with pulse regimes sometimes shortening co-occurrence time by 2,000 time units compared with press regimes and other times lengthening it by an equivalent amount (fig. 6). This difference also implies that the effects of press versus pulse disturbances on transient diversity depend on the interactions of the underlying disturbance aspects.

To understand the transient effects of pulse and press disturbances, we focused on a bistable Lotka-Volterra system where competition terms are linear. In this system, competitive exclusion is inevitable and recurring disturbance events cannot produce stable coexistence (Chesson and Huntly 1997; Fox 2013). We deliberately used this restricted system to eliminate stabilizing mechanisms and focus on the effects of the disturbance as an equalizing mechanism on coexistence (sensu Chesson 2000); while the disturbance alone cannot enable competing species to stably coexist in this system, it can delay competitive exclusion and therefore lengthen co-occurrence time. A large difference in co-occurrence time presents a challenge in distinguishing slow walks to extinctions from stable coexistence, an especially acute problem in natural systems with long generation times, such as tropical forests (Volkov et al. 2005). Furthermore, in natural systems, the longer co-occurrence time may reflect a reduction of fitness differences that may allow even weak stabilizing mechanisms to establish stable coexistence. Such interplay between coexistence mechanisms may be especially critical in competing species with evidence for weak niche differentiation, for example, barnacles along Chilean shores (Shinen and Navarrete 2014). Equalizing and stabilizing mechanisms are thought to be formally interdependent (Song et al. 2019), and we therefore expect our results to be important not only in this simple model system but also even more so in more complex natural systems, where equalizing mechanisms could complement stabilizing mechanisms to promote coexistence.

While we analyzed a linear and additive competition model, a recent body of work has employed models with nonlinear and nonadditive processes (e.g., timing [mis]-match between life history stages and disturbance events; Miller et al. 2012b), noncompetitive interactions (e.g., mutualism; Bachelot and Lee 2020), predator-prey (Commander and White 2020), and historical contingencies (i.e., the evolutionary histories of a community, the historical disturbance regimes it experienced, and the biological legacies produced; Jentsch and White 2019; Miller et al. 2021) to understand how biological complexities mediate the effects of disturbances on communities. A better understanding of the differing effects of pulse and press disturbances on diversity would require expanding our model to include these complexities to analyze how the importance of the equalizing mechanisms changes under various stabilizing mechanisms. For example, more work is needed to understand how life history traits resulting from historical disturbance regimes affect both the transient recovery dynamics and the long-term responses to disturbances (fig. 2b, dashed enclosure).

Disturbances come in many different forms in natural systems. Some disturbances, such as floods and fires, occur episodically over a relatively discrete time frame. Other disturbances—such as elevated climatic temperature, sustained landscape changes, and ocean acidification—may result in prolonged and continuously elevated death rates. Disturbance regimes are changing globally as a result of climate change. Climate change may generate both new or changed press disturbances (e.g., sustained increases in ambient temperature) and new or changed pulse disturbances (e.g., increased incidence of extreme events, such as fire), motivating the need for a more thorough and systematic understanding of how press and pulse regimes differ. While we have shown here how pulse and press regimes may differentially affect an ecological community, more work is also needed to understand how the two types of perturbation may interact to create more complex composite disturbance regimes. We have analyzed pulse and press regimes by reducing them into two component aspects (intensity and frequency), which in turn highlights where confusion or misinterpretation may arise. More work is also needed to understand how the statistical properties of each aspect (e.g., mean and variance of intensity) may feed back into the uncertainty of community dynamics.

Crucially, our work has some important empirical implications. First, our results are a cautionary tale on the complexities involved in operationally defining the basic concept of mortality rate. While calculating disturbance-related mortality rates from empirical data may seem straightforward, Sheil et al. (1995, p. 332) highlight some confusion and inconsistent methods applied within the field of ecology. They note that “in many papers the method of mortality calculation is not stated explicitly, nor can it be checked or derived from the data presented . . . or appears to be stated incorrectly.” We echo the concerns of those authors and recommend that the method of calculating mortality rates be explicitly stated and the data shared. The ability to re-calculate the rates from the data could ameliorate inconsistencies and allow for quantitative comparisons between ostensibly different empirical studies.

Second, our results can be used to design more efficient sampling strategies. We recommend that, when possible, both the disturbance aspects (e.g., disturbance frequency, intensity, duration, spatial extent) through the observational period and the population sizes (ideally both before
and after any disturbance events) should be documented. As our two approaches to modeling press disturbance show, we cannot reliably infer information about one from the other. Disturbance aspects can be measured independent of population size either directly (e.g., historical records) or indirectly (e.g., dendrochronology; Fritts and Swetnam 1989). Our results also demonstrate that studies on press and pulse disturbances require different sampling strategies: one may infer population dynamics under press disturbance by simply observing population sizes at the start and end of a study period, but the sudden changes in population size under pulse disturbances require more fine-scale observations, ideally corresponding to each disturbance event (fig. 1). Furthermore, to understand how the community changes under multiple disturbance regimes, an ecologist should use the disturbance intervals from the highest-frequency regime as the appropriate timescale to design their observations.

Third, proper design of an empirical study should depend on how the disturbances are likely to interact with the life histories of the organisms involved. For example, disturbances that occur often are more likely to interfere with reproductive output, while those that occur rarely may have either huge or no effect on reproduction if the disturbance occurs either during or between breeding seasons. Recording both the disturbance regime and the resulting biological responses instead of attempting to derive one from the other will permit stronger conclusions about the processes and mechanisms underlying their population dynamics.

These suggestions highlight the empirical difficulties we currently face in understanding how disturbances causally alter intra- and interspecific interactions, which in turn change the community structure. Until we document sufficient case studies to understand how disturbances and life history traits interact, we need to gather as much information as possible in each study; only once we have comprehensive data can we evaluate which data are less informative, thus allowing us to streamline future studies. Excitingly, many laboratory systems use press or pulse disturbance as part of the treatment (e.g., press chemostat [Fussmann et al. 2000] and pulse batch culture in microbiological experiments [Buckling et al. 2000; Hall et al. 2012]). Given the level of control available in these systems and the availability of data on the disturbance aspects, the life history traits, and the population sizes, controlled experimental systems provide a promising avenue to test and refine our understanding of the complex effects of disturbances.

Our work shows that a fair comparison between the effects of press and pulse regimes on co-occurrence time depends critically on how the press disturbance is characterized. Thus, we need to carefully consider what kind of data to collect to meaningfully assess the effects of disturbance. In some systems, we observe the endpoints with regular censuses—before and after disturbance events—but can rarely observe the system frequently enough to really see details of community dynamics as disturbances occur. In other systems, we gather information on some aspects of disturbance (e.g., time since last fire, percentage of vegetation burned) without knowing its exact effect on the population. Here, we illustrate that having only partial information can critically skew our interpretation of community dynamics and expected diversity. Our results show that how we characterize disturbance from empirical data can lead to markedly divergent interpretations of the disturbance-diversity relationship, because one method increases co-occurrence times, while the other decreases them.

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Statement of Authorship

H.I. and K.S. conceived the study. H.I. wrote and analyzed the models and wrote the first draft of the paper. All authors contributed to the interpretation of the results and edited the manuscript. K.S. and A.B. secured the funding.

Data and Code Availability

R code used for the models has been deposited in Zenodo (https://doi.org/10.5281/zenodo.5889555).

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"In a collection of acorns of Quercus prinus Linn. var. monticola Michx., found near Diamond Hill quarry, R. I., I noticed one much larger than the others, which were all large, even for the species." Left, "Dispermous Acorn, showing two plumules and two radicles." Right, "Same with covering removed, showing two seeds." From "A Dispermous Acorn" by W. W. Bailey (The American Naturalist, 1880, 14:892–893).