Chapter 4

Understanding interspecific causation in multi-species systems: development of a general approach and application to dynamics of the endangered vernal pool plant Lasthenia conjugens

## 4.1    Introduction

A common goal of both community and population ecology is estimating the proximate drivers of species abundances. However, separating correlated dynamics from causal relationships has stymied progress toward this goal, particularly in studies of communities where a multitude of species could, or could not, meaningfully influence the dynamics of every other population. While experiments can be used to distinguish and estimate the strength of causal relationships, they are often difficult to perform and rarely consider more than a handful of the possible abiotic and biotic drivers of species abundances. Regardless, a clear understanding of community structure, as well as the formulation of meaningful conservation plans, requires understanding causal relationships, particularly in response to legal protections for endangered species [144].

The most common way to model proximate effects in multi-species systems is with a community matrix. The conceptual framework that forms the basis for this approach rests on Lotka-Volterra dynamics [152, 247]. Consider a predator $Y$ and its prey $X$, whose rates of change in abundance are governed by the equations $\frac{dX}{dt} = Ax - Bxy$ and $\frac{dY}{dt} = Cxy - Dy$. Community matrices combine all pairs of interactions into a square matrix with density dependent terms along the diagonal: $\begin{bmatrix} A & -B \\ C & -D \end{bmatrix}$. Unfortunately there is no consensus on how to estimate these interaction strengths. There are established protocols for many direct interactions, such as using gut contents

to estimate predation rates [154] or ectoparasite loads to estimate parasitism [227], but no consensus on how to estimate indirect interactions (e.g. competition, mutualism). The myriad of methods that do exist generally utilize trait comparisons [137, 199], phylogenetic similarities [202, 243], or geographic overlap/co-occurrence patterns [7, 13, 181, 216]. These all have merit, but they do not separate causal relationships from associative ones. Even time series analyses [57, 114] tend to ignore the "inescapable fact that probability theory, the official mathematical language of many empirical sciences, does not permit us to express sentences such as 'Mud does not cause rain' " [192].

More recently, causality itself has been proposed as a currency of interaction that can infer indirect interactions from observational data. While there is similarly no agreement on how best to infer causality, and no single universally applicable method, those that do exist all attempt to identify causal relationships even in the face of confounding correlations of dynamics due to common forcing from factors such as weather. This is especially important in ecology where multicollinearity is ubiquitous and too often inappropriately modeled with generalized linear models and post-hoc information theoretic model selection [23, 90]. Unfortunately, the relationship between causal strength and interaction strength is poorly understood, and likely varies between causal inferences. In addition, the outputs of all causal tests with which we are familiar are not translatable into per capita effects, such as those that comprise the community matrix, or any similar direct measure of effects on dynamics [143, 179]. As such, these methods do not reliably provide estimates of interaction strength that can be directly applied to estimate rates of change of a target species' abundance.

A second major limitation of the usual ways of characterizing drivers of species abundances is that these effects are likely to shift with densities as well as environmental conditions. As Paine showed experimentally [258] and argued as a general point [186], the natural history of virtually all communities makes a single static community matrix inadequate. However, using typically available ecological data to make estimates not only of multiple species interactions, but also the variation in these effects, is a daunting challenge. One recently suggested approach is Empirical Dynamic Modeling (EDM; [259]), which has shown promise as a nonparametric framework capable

of estimating dynamic interactions [57]. EDM methods eschew a precise mathematical model of a system in favor of empirically reconstructing the system's dynamics, which is called an attractor or manifold. In this framework each species and abiotic factor is treated as an axis in a higher-dimensional plot. Through time this plot maps the system's "evolution semi-flow" [234]. These evolving flows are often too chaotic to be described as a mathematical function, but if the manifold is sufficiently dense (well sampled, or filled in) it can be used to recover reliable estimates of the system's instantaneous dynamics. These estimates are Jacobians, or a kind of community matrix containing all pairwise interactions in the system [143]. Rather than a single matrix for the whole system, this approach generates a time series of Jacobians, one from the perspective of each data point. This sequence is called an S-map [231]. While this approach has shown promise in its dynamic characterizations of community interactions [57], it does not allow a direct test to separate causation from correlation.

Thus, while they attack two fundamental shortcomings of community interaction character-izations, causal inference and S-maps addresses the tendency of species abundances to covary and their interactions to change separately. Here we develop a novel combination of these methods. Our overall goal is to look across large numbers of possibly interacting species and quantify the influences of the most likely drivers of the dynamics of a target species. Specifically, we focus on the following: (i) Developing a method that combines causal inference and S-maps in a way that yields more flexible and rigorous approaches to assessing the strength of causal interspecific interactions, (ii) using this approach to analyze a typical system in which time series data on abundances of mul-tiple species are available but experimental data are not, and (iii) comparing the results we obtain against those from a non-causal S-map as well as data from other studies of the same system to gauge what improvements or shortcomings our combination of causal and dynamic inference has. For this work, we focus on Lasthenia conjugens in a vernal pool system with 14 years of data on 16 species in 247 pools. While here we focus exclusively on the effects other species have on Lasthenia conjugens, as a way to address the conservation of a federally listed species, the broader goal of our work is to engender this type of analysis for entire communities.

## 4.2      Methods

### 4.2.1      Data

We use causally-filtered S-maps to study interspecific drivers of endangered Lasthenia con-
jugens populations growing in vernal pools at Travis Air Force Base (AFB) in Solano County,
California, USA in the Sacramento Valley near the town of Fairfield (38°15'00" N, 122°,00'00" W,
6 m elevation). This area receives approximately 50 cm of annual precipitation, almost entirely
during the wet season from December to April. The site has approximately 100 naturally occurring
vernal pools which are host to one of the few remaining populations of the annual plant Lasthe-
nia conjugens (Contra Costa goldfields, Asteraceae: Heliantheae). However, all of the data used
here come from 247 experimentally constructed pools previously used to study Lasthenia conjugens
restoration, invasion, and community assembly [41–43]. These pools were constructed in December
1999 and seeded in 1999, 2000, and 2001. We have used data from 2002 to 2016, during which time
Lasthenia conjugens declined in most of the pools.

In each of these 15 years all 247 pools were sampled using a 100 cell quadrat, where the
frequency of each species was quantified as the percent of cells in which an individual of that species
was visible. Note that an individual plant can occupy more than one cell, as can multiple individuals
of different species. So while each species ranged between 0 and 100 percent, cumulative community
composition ranged from 0 to 400 percent. Of these, 0 and 100 percent were the most common,
with cumulative compositions between them uniformly distributed and cumulative compositions
greater than 100 percent exponentially declining.

The most important abiotic driver of population dynamics in this system is water [41–43, 82].
Lasthenia and most other species in this system are winter annuals (or perennials with similar
phenology). Germination starts with the fall rains, and growth is limited in the spring by dry-
down following cessation of the winter rains. To capture the potentially differing effects of fall and
spring rainfall, we divided annual precipitation into early (October - December) and late (Januray
- April) periods. Rainfall data was left in its original units (inches), so while these models included

their effects, their magnitudes are not comparable with the inferred interspecific effects. See Fig. C.5 for the direct effects of early and late season rainfall on Lasthenia conjugens.

### 4.2.2 S-maps

S-maps [57, 231, 259] are sequences of Jacobians, or matrices of interactions where the $ij_\text{th}$ element is the partial derivative $\frac{\partial i}{\partial j}$ for species $i$ and $j$, and the $ii_\text{th}$ elements along the diagonal are population growth rates of species $i$. These are the same values in one of the most used kinds of community matrix, a common way of representing species interactions [143, 179]. However, a single static community matrix is usually estimated and analyzed, while S-maps contain one Jacobian for each observation. These Jacobians are calculated as a multivariate regression predicting the system's transition from $X_t$ to $X_{t+1}$, but where every other observation $X_k$ has weight $w_k$ equal to its exponentially-weighted Euclidean distance $\| \cdot \|$ to the system's state at time $t$.

$$w_{kt} = \exp\frac{-\theta\|X_k - X_t\|}{\|X_k - X_t\|} \tag{4.1}$$

We used an exponential decay of $\theta = 10.22$ which minimized the normalized mean absolute error (nMAE) of leave-one-out cross validation in accordance with [57]. This distance is not temporal, or spatial in the case of spatial replication, but rather the distance in the state-space where the system's manifold was reconstructed, and is scaled exponentially because system manifolds are often nonlinear and even chaotic [97, 98, 239] In accordance with [57], the focal observation is left out from each multivariate regression. Fig. C.7 shows that even the strongest weight in each S-map tends to be close to zero (the maximum is one because $e^0 = 1$), and falls off exponentially. Using these weights dramatically improves the estimated partial derivatives in each Jacobian, especially for communities with chaotic dynamics occurring faster than they are observed [57]. The strength of this weighting relative to the state-space distances between observations can be seen in Fig. C.7. In this study these weights spanned all observations, across all 14 years and also all 247 pools, as there is evidence in support of combining spatial and temporal replication to infer causality [36].

This works by finding the regression estimates

$$\hat{\beta}_t = (X^\mathsf{T}\langle W_t\rangle X)^{-1}X^\mathsf{T}\langle W_t\rangle Y \tag{4.2}$$

where $\langle W_t\rangle$ is a square matrix with weights $w_{kt}$ on its diagonal and $\hat{\beta}$ is the least squares solution to $Y = \beta X$. These coefficients, $\hat{\beta}_t$, are the estimates of the partial derivatives $\frac{\partial i}{\partial j}$ in the community matrix.

Eq. 4.2 is the general formula for calculating an S-map, but the data on the Lasthenia conjugens vernal pool plant community require a more complicated model because species frequencies were quantified as the percent of cells in a quadrat they occupied. We converted this data to densities, by normalizing to unity, and then used weighted beta regression. Lasthenia conjugens was often unobserved, and sometimes occurred in all 100 quadrat cells, so we used weighted zero-one-inflated beta regressions to characterize effects on Lasthenia conjugens densities, which was accomplished with the R package GAMLSS [203]. In these models, we fit the future density of Lasthenia conjugens in pool $p$ as a function of its past density in the same pool, the past densities of other species in the same pool, and the early and late rainfall that year. Pool size (small, medium, or large) and pool ID were included as categorical variables.

$$L_{p_{t+1}} \sim L_{p_t} + X_{1p_t} + \cdots + X_{Np_t} + \text{Rainfall}_{\text{early}_t} + \text{Rainfall}_{\text{late}_t} + \text{factor}(\text{Pool Size})_p + \text{factor}(\text{Pool ID}_p) \tag{4.3}$$

### 4.2.3    Causality

Calculating the Jacobians in an S-map with multivariate regression makes them susceptible to "mirage" correlations, where variables that do not interact covary because of common drivers [90]. This in turn makes any individual $\frac{\partial i}{\partial j}$ unreliable as an indicator of actual causal effects. Ideally, then, we would use a method of assessing true causation to filter or weight the results of an S-map analysis. Convergent Cross Mapping (CCM; [232]) is a natural choice because it too derives from

the EDM framework. Unfortunately, CCM assumes a degree of deterministic coupling (chaotic nonlinear dynamics) that is not ubiquitous in ecological systems. Often many observed species in a community will not be testable with CCM [141], and weights for predictor variables should include all predictors. Additionally, both CCM and Granger causality [91] collapse the data's temporal component down to a single value. Using one of them as a weight for the predictors in an S-map therefore results in a single weight for each predictor across all time points, preventing the S-map from capturing dynamic interactions. Liang's information flow [150] is extremely promising as an alternative in it's adherence to the principle of nil causality, where "an event is not causal to another event if the evolution of the latter does not depend on the former", but is currently only applicable to two-dimensional systems.

We have instead used a well-studied information theoretic measure of causality which first assumes no information is being transfered between a potential causer and causee and then measures how wrong this assumption is as a Kullback entropy [136], also known as a KL divergence and here denoted with the letter $T$ because the most common formalism, Schreiber's [214], called this idea transfer entropy.

$$T_{\text{species B} \rightarrow \text{species A}} = \sum_t p(A_{t+1}, A_t^{(c)}, B_t^{(d)}) \log \frac{p(A_{t+1}|A_t^{(c)}, B_t^{(d)})}{p(A_{t+1}|A_t^{(c)})} \qquad (4.4)$$

Here $A$ and $B$ are species abundances (or densities) and $p$ is the probability of the system being in a particular state. Note that this state spans multiple time points. Schreiber described the exponents $c$ and $d$ as the order the Markov system assumed in modeling the data in discrete time steps, from $t$ to $t+1$. Within the EDM framework these values can be calculated as the manifold's embedding dimension, such that $A_t^{(c)} = \{A_t, A_{t-\tau}, A_{t-2\tau}, \cdots, A_{t-(c-1)\tau}\}$. The value of $c$ and $d$ are challenging to determine and larger values make calculating the probabilities that comprise transfer entropy computationally intractable. Fortunately, the vernal pool plant community studied here contains mostly annual plants making $c = d = 1$ a natural choice.

Schreiber recommends approximating the probabilities that comprise transfer entropy using

generalized correlation integrals estimated with a step kernel $\Theta$ averaged across all observations.

$$\hat{p}_r(A_{t+1}, A_t, B_t) = \frac{1}{|t'| - 1} \sum_{t' \neq t} \Theta \left( \begin{vmatrix} A_{t+1} - A_{t'+1} \\ A_t - A_{t'} \\ B_t - B_{t'} \end{vmatrix} - r \right) \tag{4.5}$$

This estimates each probability as the proportion of system states that were within some distance $r$ from the state of interest, namely $\{A_{t+1}, A_t, B_t\}$. We have instead calculated these probabilities using an exponentially decaying kernel estimation where each observation gives every other observation probability mass exponentially weighted by their Euclidean distance, to parallel the weighting used in S-maps (Eq. 4.1).

$$\hat{p}_r(A_{t+1}, A_t, B_t) = \frac{1}{|t'| - 1} \sum_{t'} \exp \frac{-\theta \|(A_{t+1}, A_t, B_t) - (A_{t'+1}, A_{t'}, B_{t'})\|}{\|(A_{t+1}, A_t, B_t) - (A_{t'+1}, A_{t'}, B_{t'})\|} \tag{4.6}$$

The decay parameter $\theta$ serves a similar purpose here to the exponential weighting of data in S-maps: to share information between observations using the Euclidean distance between them. We have therefore used the same value for both: $\theta = 10.22$. Note that this works identically for the other two probabilities needed to calculate transfer entropy, $p(A_{t+1}|A_t, B_t) = \frac{p(A_{t+1}, A_t, B_t)}{p(A_t, B_t)}$ and $p(A_{t+1}|A_t) = \frac{p(A_{t+1}, A_t)}{p(A_t)}$, only with two and one-dimensional distances.

### 4.2.4    Causally-filtered S-maps

Transfer entropy has three properties that make it especially well suited to causally correcting S-maps. (i) It makes no assumptions about the dynamics of the time series of species $A$ or $B$ and is therefore universally applicable. (ii) Transfer entropy can account for common drivers $Z$ of species $A$ and $B$ "by conditioning the probabilities under the logarithm to each $z_n \in Z$ as well". [214] For example, $T_{A \rightarrow B} = \sum_t p(A_{t+1}, A_t^{(c)}, B_t^{(d)}) \log \frac{p(A_{t+1}|A_t^{(c)}, B_t^{(d)}, z_t^{(e)})}{p(A_{t+1}|A_t^{(c)}, z_t^{(e)})}$ prevents species $A$ from appearing causal to species $B$ when they were both caused by a common environmental driver $z$, and therefore contain overlapping information irrelevant to their interspecific interactions [222]. (iii) Transfer entropy is a sum. By splitting this sum apart we can quantify causality at the temporal resolution of the data. While this almost certainly reduces its sensitivity, each calculation still contains

information about every observation. The features of this fine-grained use of transfer entropy have yet to be studied and deserve further attention.

A temporally split transfer entropy therefore forms a one-to-one correspondence (bijection) with an S-map. We considered two ways of combining these two analyses. The first was a causal filter where entries in the S-map Jacobians are proportional to the magnitude of the corresponding marginal transfer entropies. We decided against this approach because of a desire to decouple the amount of information moving between variables and their biological effects on each other.

Instead, we calculated the Jacobian entries as the expected S-map coefficients across all possible community compositions where species are included proportional to their marginal transfer entropies. This models the system as a weighted average across an infinite number of realizations of the target species' dynamics, here Lasthenia conjugens, but in each realization only some of the other species are included, with a probability proportional to their marginal transfer entropy. Simulating this approach is intractable in this system because many of the species have relatively tiny transfer entropies with Lasthenia conjugens and therefore never occur by chance. However, the expected value of each interspecific interaction can be calculated as a weighted average of S-map coefficients, with one S-map for each set $\rho$ of observed species $x \in X$ in the power set $\mathcal{P}(X)$ of all observed species. Each S-map is weighted by the product of the transfer entropies (normalized by $\varphi$) from the species $x$ in its corresponding set $\rho$ to Lasthenia conjugens, denoted by the transfer entropy $T_x$. We excluded the null set $\varnothing$ such that Lasthenia conjugens had to interact with at least one of the observed species. Note that this treats $T_{x_i}$ as independent from all $T_{x_{j \neq i}}$.

Causally-filtered S-map estimates $\hat{\beta}_c$ of the interactions of variables $x \in X$ on a variable $y$ of interest, here the density of Lasthenia conjugens, at time $t$ are therefore defined as the regression

estimates:

$$\hat{\beta}_{ct} = \frac{1}{|\mathcal{P}(X)| - 1} \sum_{\rho \in \mathcal{P}(X) \setminus \varnothing} \left[ \left( \varphi \prod_{x \in \rho} T_x \right) (X_\rho^\mathsf{T} \langle W_{\rho_t} \rangle X_\rho)^{-1} X_\rho^\mathsf{T} \langle W_{\rho_t} \rangle Y \right] \tag{4.7}$$

<center>Causal Weights     S-map Weights</center>
<center>Average Across Possible Interactions     Least Squares Regression</center>

The weights on the diagonal of the matrices $\langle W_{\rho_t} \rangle$ are at the heart of this method. They vary both for each time $t$, in accordance with the S-map method, and for each subset of species observed at each time $t$, proportional to the product of their marginal transfer entropies. As with traditional S-maps, these weights span all observations, across all 14 years and also all 247 pools, which treats temporal and spatial replication as independent observations of the community's dynamics. While this assumption is almost never valid, it makes estimates of the probabilities that comprise transfer entropy (Eq. 4.4) more robust, and there is evidence in support of combining spatial and temporal replication to infer causality [36].

## 4.3    Results

To introduce the types of results and inferences from this method, we first discuss the results of the causally-weighted S-maps for just one pool. Predictions from Pool 300 provide a typical example of the multicollinearity in the dynamics of these vernal pool plant populations, how this results in unreliable S-map estimates of interaction strengths, and how our causally-filtered extension corrects for this. As seen in the top panel of Fig. 4.1, Lasthenia conjugens remained at very low densities until 2007 when it then rose to over a quarter of the community's composition before crashing in 2010. The population rebounded the following year, rising to its highest density of 0.5 in 2012, before crashing again the following year. This trend was not unique to Lasthenia conjugens. Downingia concolor, Crassula aquatica, and the exotic species Lolium multiflorium

similarly rose and fell in density twice. Separable models, like regression, cannot distinguish causes from covariates, even when weighted by community state similarity as S-maps are. The result is a parsing of variance across all covariates, including those that are not causally related. This can be seen in the difference between the middle and bottom panels in Fig. 4.1. The uncorrected S-map (middle panel) suggests that Lasthenia conjugens had a small ($< 10$) and mostly constant annual growth rate, and that interspecific interactions were mostly unimportant except for a few very important exceptions which drove its dynamics. Achyrachaena mollis helped Lasthenia conjugens establish in this pool, but along with Lupinus bicolor had a strong negative effect on Lasthenia conjugens in 2008. Curiously this competition was not reflected in the dynamics of Lasthenia conjugens which increased in density. More recently, Lasthenia conjugens appeared only to interact with Plagiobothrys stipitatus and Psilocarphus oregonus.

These estimates are unconvincing for two reasons. First, previous analyses show that Lolium multiflorium and Hordeum marinum, the two exotic species, played an important role in Lasthenia conjugens' decline [42], but the S-map did not recover these interaction. Second, while interspecific interactions are dynamic, constant weak interactions punctuated by strong ephemeral ones with different species seem biologically unrealistic. Consider the complexity of mechanisms which would produce near identical weak interactions with a dozen co-occurring species most of the time, but then momentarily strong interactions with alternating individual species. This is more likely a statistical artifact.

The causally-filtered S-map offers a more parsimonious explanation of Lasthenia conjugens' dynamics. As seen in the bottom panel of Fig. 4.1, they were more a result of intraspecific interactions, which were likely driven by early- and late-season rainfall which had strong effects on both Lasthenia conjugens' annual growth rate (Fig. C.4) and the interspecific effects of other species in the community on Lasthenia conjugens (Fig. 4.5). However rainfall was measured in inches making the resulting strengths of early- and late-season rainfall on Lasthenia conjugens (Fig. C.5) incomparable with (smaller than) the inferred interspecific interaction strengths. Also more parsimonious was the finding that those interspecific interactions that were present were consistent,
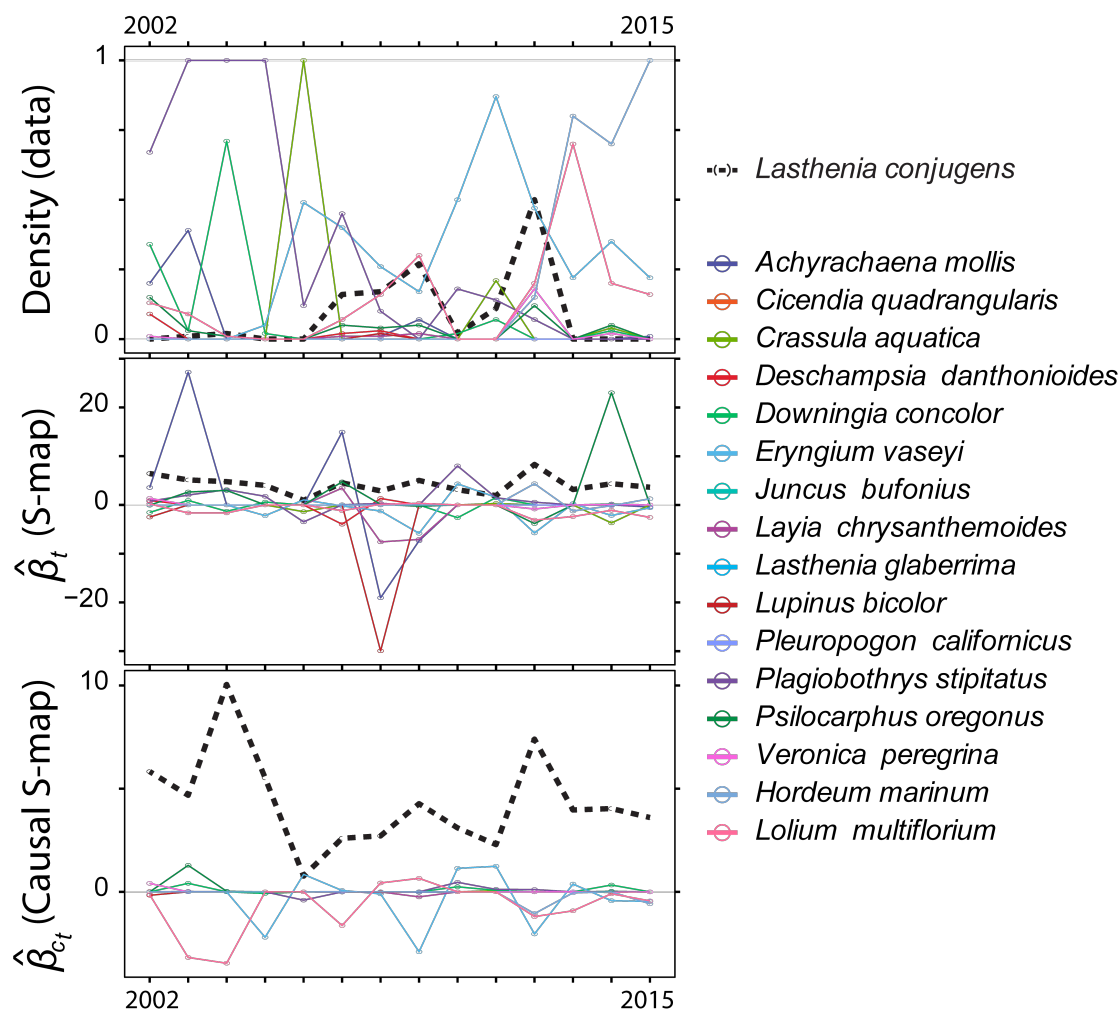
Figure 4.1: Observed population fluctuations and inferred interactions in vernal pool 300. Top) Observed densities of Lasthenia conjugens, 14 other native plant species, and 2 exotic plant species from 2002 to 2015. Middle) Interactions between Lasthenia conjugens, the 16 other plant species, and both early and late season precipitation inferred using an S-map. These values are the $\hat{Beta}_t$ coefficients in the S-map's multivariate zero-one-inflated beta regressions, which measure the effect of a change in the density of each species on the annual growth rate of Lasthenia conjugens. These inferred interactions incorrectly parse Lasthenia conjugens' variance across covarying but non-interacting species. Bottom) Identical to the middle panel only using causally-filtered S-maps, which appear to more correctly parse the community's covariance structure to identify Lasthenia conjugens' independence, and the exotic Lolium multiflorium and perennial Eryngium vaseyi as the main interspecific drivers of its dynamics.

and with species we know from previous work [42, 73] did interact with Lasthenia conjugens: the exotic Lolium multiflorium and Eryngium vaseyi which was the only observed perennial species. As Fig. 4.2 shows, these trends were consistent across all 247 pools, where the exotic and perennial species had the strongest effects on Lasthenia conjugens.

S-maps, and our causal extension of them, are powerful in that they estimate interactions at the same resolution as the underlying data. We can therefore more closely examine patterns in the interactions of the exotic and perennial species with Lasthenia conjugens. The following two sections are devoted to dissecting these results for the entire dataset, though not for Hordeum marinum which only had a strong effect on Lasthenia conjugens in 2004 (Fig. C.1).

### 4.3.1    Lolium multiflorium

Lolium multiflorium's effect on Lasthenia conjugens was spatially uniform (Fig. 4.3, top right panel). While there was variance among pools in the strength of its interaction, this variance was not directional. This contrasts with the 16 native species growing in these pools with Lasthenia conjugens which had a tendency to interact more strongly in more northern pools (Fig. C.2). We suspect this resulted from a northern downward slope. This slope is difficult to see with the naked eye and therefore unlikely to effect dispersal, but it could have effected drainage across the site leading to an accumulation of water in the more northern pools.

While Lolium multiflorium did not co-occur at high densities with Lasthenia conjugens, its effect on Lasthenia conjugens was independent of either of their densities (Fig. 4.3, bottom left panel). It could be that Lolium multiflorium's thatch accumulated too quickly in these pools for either of their densities to matter. Alternatively, this system may be driven by rainfall to such an extent that the co-occurrence of other species is comparatively unimportant to the survival and reproduction of Lasthenia conjugens. The top left and bottom right panels of Fig. 4.3 show that these interactions were predominantly water-mediated, with the strongest interactions occurring at intermediate levels of both early and late season rainfall. Lasthenia conjugens' growth rate was highest at intermediate levels of precipitation (Fig. C.4), making it also the most susceptible to
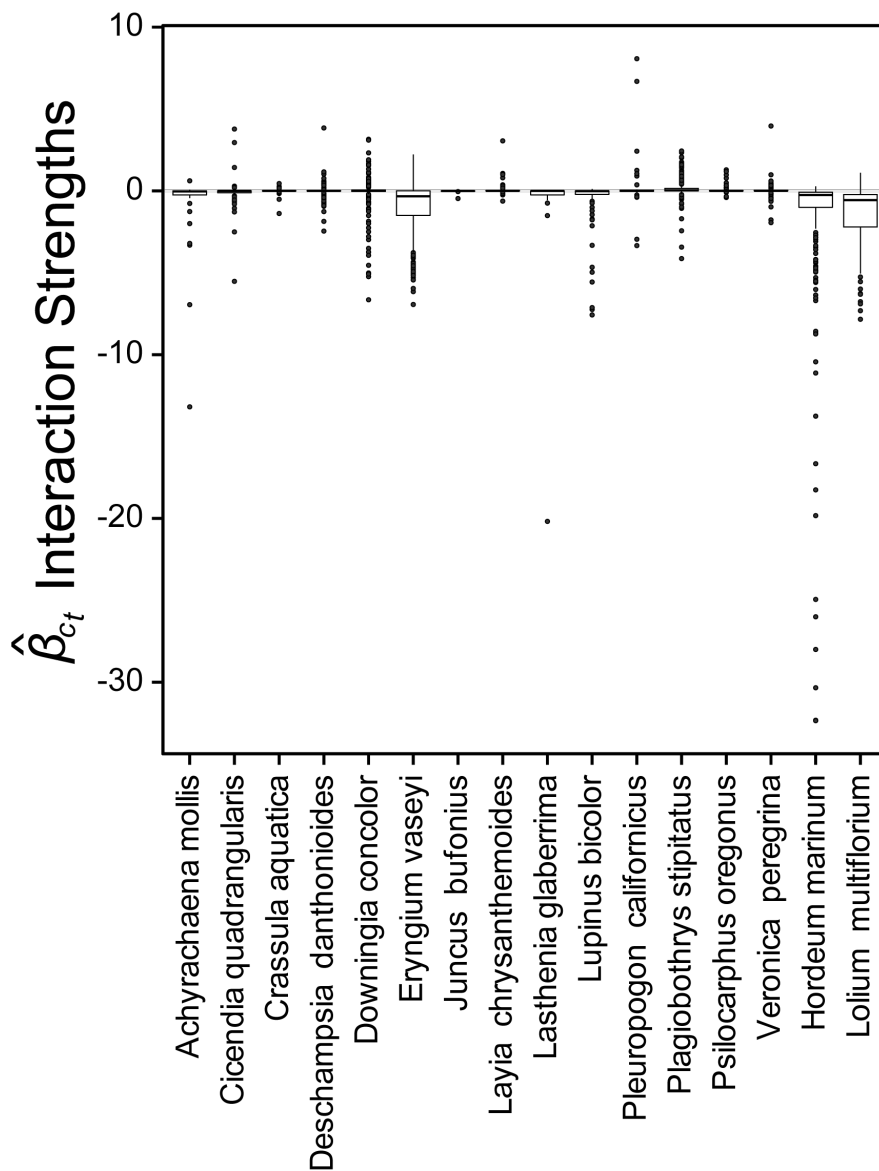
Figure 4.2: Interspecific effects on Lasthenia conjugens, inferred with causally-filtered S-maps, aggregated across all 247 pools for all 14 years. Hordeum marinum's effect on Lasthenia conjugens mostly occurred in 2004 (Fig. C.1).

Figure 4.3: Aggregate effects of Lolium multiflorium on Lasthenia conjugens' annual growth rate ($\hat{\beta}_c$). Top Left) Annual interspecific interactions. Boxes span interquartile ranges (IQR), with the inside bar at medians and whiskers extending to the most extreme data within $\pm 1.5 * \text{IQR}$. Top Right) Average interspecific interactions in each vernal pool. Only pools where Lolium multiflorium was observed are plotted. Bottom Left) Density-mediated interactions between Lolium multiflorium and Lasthenia conjugens. Bottom Right) Interactions as a function of early- and late-season precipitation.

interspecific effects. In the first five years of observations, up to 2006, rainfall drove this interaction. As the years got wetter Lolium multiflorium's effect on Lasthenia conjugens weakened and almost disappeared, before strengthening in the drier 2006 and 2007. Lolium multiflorium antagonized Lasthenia conjugens at lower levels of precipitation, but the fluctuations in precipitation between 2010 and 2015 had little effect on Lolium multiflorium' effect on Lasthenia conjugens.

### 4.3.2   Eryngium vaseyi

Eryngium vaseyi's effect on Lasthenia conjugens was also spatially homogenous, with four exceptions. In four pools in the north and east of the group south of the abandoned airstrip Erygnium vaseyi benefited Lasthenia conjugens, on average. Drainage likely cannot explain these outliers because the effect was not present in surrounding pools, and there was no directional gradient.

Unlike with Lolium multiflorium, Eryngium vaseyi's interactions with Lasthenia conjugens was density dependent, but only Eryngium vaseyi's density effected these interactions. In a two way regression explaining Eryngium vaseyi's interactions with Lasthenia conjugens, Lasthenia conjugens' density had a p-value of 0.65, Eryngium vaseyi's density had a p-value of 0.004, and the interaction between their densities had a p-value of 0.056. This can be seen in the preponderance of blue points along the vertical axis, where Eryngium vaseyi's density was close to zero. This may be evidence that, as a perennial plant, Eryngium vaseyi alters the physical makeup of vernal pools in ways that are advantageous to Lasthenia conjugens at low densities, or that Erygnium vaseyi prevented exotic establishment or the accumulation of their thatch. Eryngium vaseyi and Lolium multiflorium tended not to co-occur and showed a complimentary tradeoff in the strength of their effects on Lasthenia conjugens (Fig. C.6). However, Eryngium vaseyi occurred at low densities even when Lolium multiflorium occurred at high densities, possibly keeping Lolium multiflorium's thatch from completely hindering Lasthenia conjugens survival.

Water mediated Eryngium vaseyi's effect on Lasthenia conjugens the same as it did Lolium multiflorium's (Fig. 4.4, bottom right panel). It had the strongest negative effect on Lasthenia
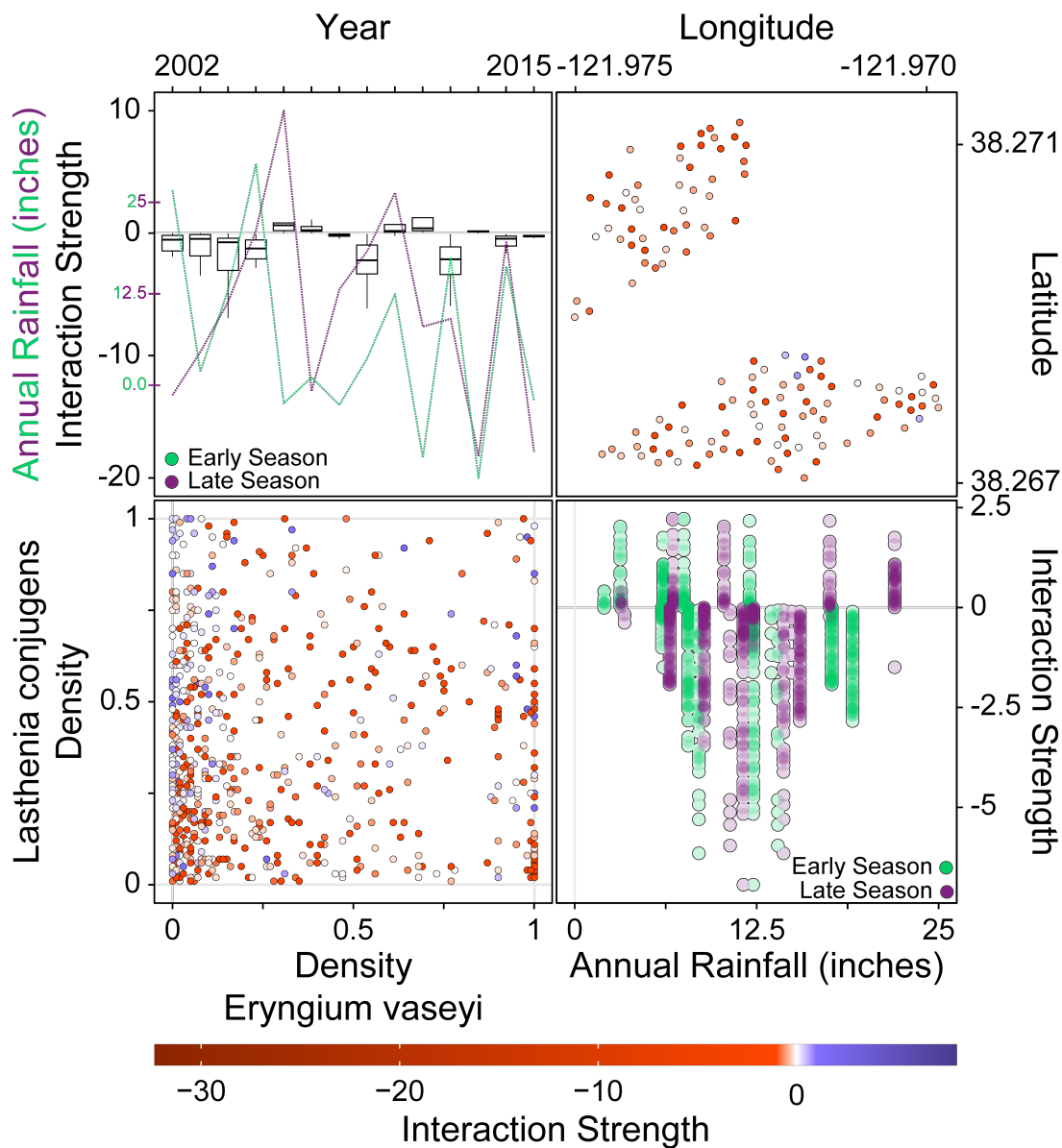
Figure 4.4: Aggregate effects of Eryngium vaseyi on Lasthenia conjugens' annual growth rate ($\hat{\beta}_c$). Top Left) Annual interspecific interactions. Boxes span interquartile ranges (IQR), with the inside bar at medians and whiskers extending to the most extreme data within $\pm 1.5 * $ IQR. Top Right) Average interspecific interactions in each vernal pool. Only pools where Eryngium vaseyi was observed are plotted. Bottom Left) Density-mediated interactions between Eryngium vaseyi and Lasthenia conjugens. Bottom Right) Interactions as a function of early- and late-season precipitation.

conjugens at intermediate levels of precipitation, and its weaker positive effects, which were more numerous than Lolium multiflorium's, were water-independent. The top left panel of Fig. 4.4 indicates that late season rain drove these interactions. 2006 and 2010 were the wettest years between January and April (the late season) and were also years where Eryngium vaseyi's effect on Lasthenia conjugens was positive. This trend was inconsistent though. 2011 was dry all the way from October through April (early- and late-season) yet these interactions were still positive.

### 4.3.3    Water-Mediated Interactions

It is no surprise that water mediated interspecific interactions between these vernal pool plant populations, as their life histories have co-evolved with the annual rainfall cycle. We therefore also considered how it mediated all of Lasthenia conjugens' interspecific interactions.

As Fig. 4.5 shows, the species that interacted with Lasthenia conjugens fell into two general kinds of interaction strength distributions: stronger interactions at intermediate levels of precipitation and stronger interactions at extreme levels of precipitation. The three strongest interactors, the perennial Eryngium vaseyi and the two exotics Hordeum marinum and Lolium multiflorium, were all in the first category. Those species that fell into the second category also differed in being inconsistent in the way they interacted with Lasthenia conjugens. Downingia concolor and Plagiobothrys stipitatus were like the perennial and two exotic species in that they had a negative effect on Lasthenia conjugens, but Pleuropogon californicus and Deschampsia danthonioides helped Lasthenia conjugens. Also unlike those species in the first category, the sign of these species' interactions tended to flip at intermediate levels of precipitation.

### 4.4    Discussion

We have presented a way to infer traditional ecological interaction strengths amidst multi-collinearity in a real community of conservation interest by combining S-maps [57], which are time series of Jacobians (matrices of pairwise interaction strengths) with transfer entropies [214], which measure causality. These causally-filtered S-maps can be inferred from observational data and esti-
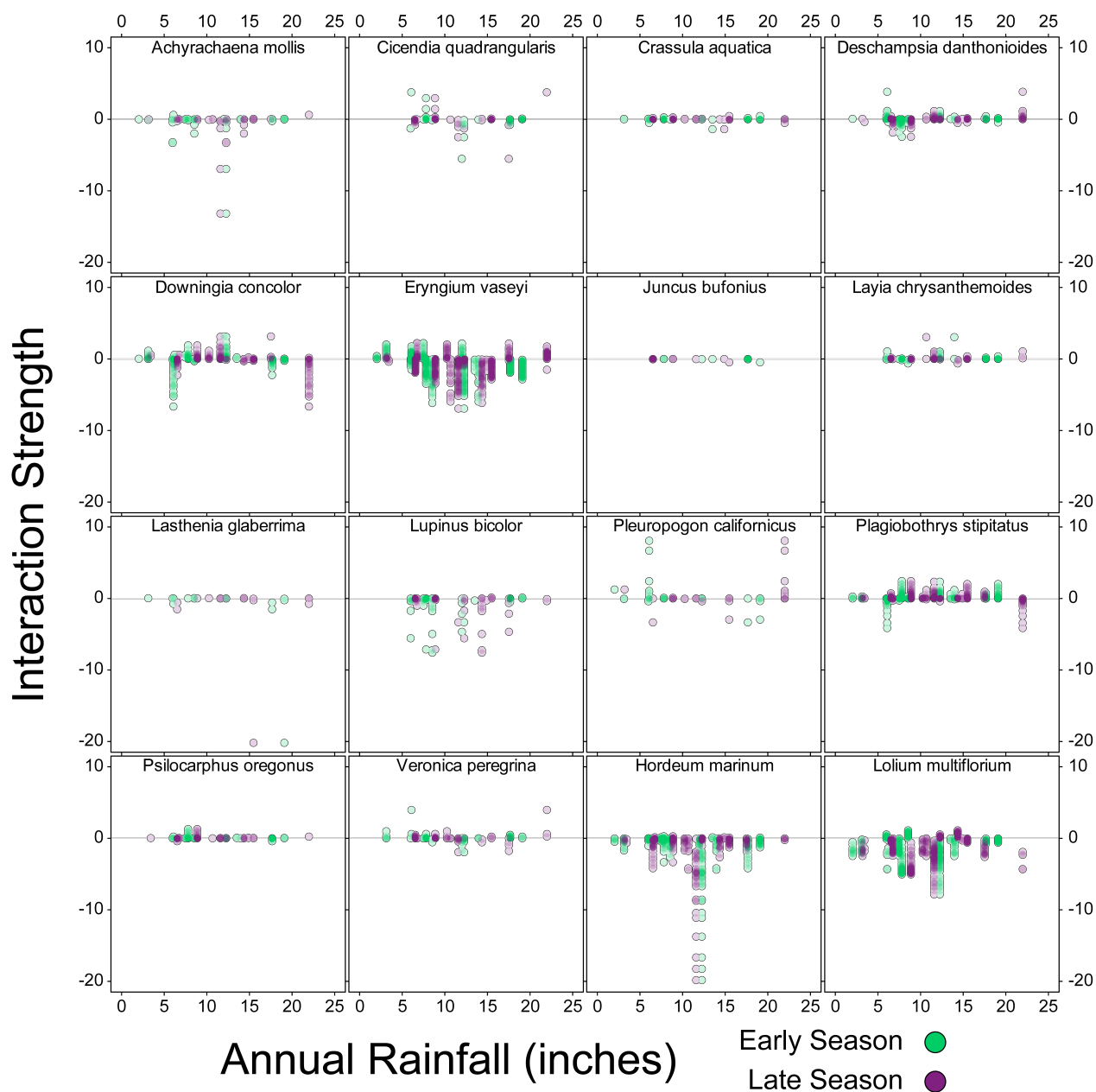
Figure 4.5: Lasthenia conjugens' interspecific interactions as a function of early- and late-season precipitation, defined as their effect on Lasthenia conjugens' annual growth rate ($\hat{\beta}_c$). The darkness of the colors in the legend are 5 or more overlapping points.

mate interaction strengths at the same resolution as the data being used. As we have demonstrated, this approach offers a way to infer drivers of important species, such as the endangered Californian vernal pool plant Lasthenia conjugens, in communities with substantial covariance structures without the benefit of costly or impractical experimental manipulations.

Inferring interaction strengths at the resolution of individual data points, arrayed spatially and temporally, rather than with a single averaged community matrix, offers tremendous advantages. We identified interspecific drivers of the endangered vernal pool plant Lasthenia conjugens in time and space, as well as how species density and levels of early and late season precipitation mediated these interactions. While the importance of the two exotic species (Lolium multiflorium and Hordeum marinum) was already known [42], our approach offers a more nuanced interpretation of when and how these species effected Lasthenia conjugens. For instance, the strengths of these two interspecific interactions were largely dependent on early and late season rainfall, with stronger antagonism at intermediate levels. This drove the early takeover of these vernal pool communities by Lolium multiflorium, which creates a thatch [73] that prevents native species like Lasthenia conjugens from rebounding in drier or wetter years, or using their seedbank to re-establish. Interestingly, many of the other native species interacted with Lasthenia conjugens more strongly in those extreme dry or wet years, some antagonistically but some beneficially.

The high resolution of interactions inferred by both S-maps and our causal extension allows community dynamics to be mapped precisely through space and time. For instance, we found evidence of interactions being more beneficial to Lasthenia conjugens in more northern pools, though with exceptions such as Veronica peregrina (Fig. C.2). We were also able to identify transient water-mediated interspecific dynamics, such as with Lolium multiflorium before and after 2006. Across all 14 native and 2 exotic species, we found that interspecific effects on Lasthenia conjugens were the exception (Fig. C.1). Hordeum marinum, the other exotic species, mostly exerted a small negative effect on Lasthenia conjugens, but in 2004 caused dramatic declines. This kind of punctuated interspecific interactivity also occurred with Achyrachaena mollis, Downingia concolor, and Lasthenia glaberrima, emphasizing the danger of using a single community matrix to

model interspecific interactions. Similarly, an historical reliance on individual community matrices has hindered our understanding of density dependence, which has been exacerbated by the ways multicollinearity masks direct effects. Using causally-filtered S-maps we were able to show that, with the exception of Eryngium vaseyi, density dependence was largely unimportant to interspecific effects on Lasthenia conjugens.

Causally-filtered S-maps add to a growing body of causal inference methods in ecology that can be used to infer ecological processes in the face of noisy data often collected at scales larger than those at which the processes occur. While there is evidence that we can and should make conservation decisions with these methods [55, 56, 229], there is still no unified theory of causality, and often species within a single system will meet the assumptions of different causal methods differently [141]. The closest to a unified theory of causality is called information flow, or information transfer, [148] which is the only theory we are aware of that adheres to the principle of nil causality, that "an event is not causal to another event if the evolution of the latter does not depend on the former" [150]. Unfortunately information flow has only been developed to the stage where it is usable for real data from two-dimensional systems [148]. Additionally, none of the causal theories we are aware of explicitly address the relationship between causal strength and interaction strength. This is especially important when combining causal inference with methods like S-maps that infer community matrices of interaction strengths. As mentioned in the Causally-filtered S-maps section of the Methods, our formulation of a causal correction for S-maps decouples the strength of causation from the resulting per capita interaction strengths, but often these are assumed to be identical. This was not the case for transfer entropies and per density interaction coefficients in this system (Fig. C.8), where a small or large interspecific transfer of information sometimes manifested a large or small per capita biological effect respectively. This relationship is complicated by causal noise and the resulting distribution around nil causality (Fig. C.8). Observation and process noise create causal noise, but we are currently unaware of a null model for causality which accounts for this. Another complication is that some causal inferences measure the certainty of causation, not its strength. Convergent Cross Mapping (CCM) is one such method [232]. These inferences should

be explicitly decoupled in future work that estimates interaction strength using causal inference.

An accompanying measure of uncertainty would strengthen both the original S-map method and our causal extension. While the goal of these methods is to infer dynamic interactions, it may be that in noisy and poorly-sampled systems the exact values they produce are not reliable. In the system studied here, densities were measured using a single quadrat per pool per year, which incorrectly assumed homogeneity. The reappearance of Lasthenia conjugens in pools following years where it was absent may reflect may reflect complicated seed bank dynamics at play in these pools [41] and a storage effect that helps plants survive stressful years [72, 250]. It may also be dispersal from other individuals in a part of the pool that was not sampled. A sequence of binary (unweighted) networks, where interspecific interactions are classified as present or absent at each time point, would better model these unobserved dynamics than a single weighted average matrix. These sequences could be produced by repeatedly randomizing the data to bootstrap a distribution of transfer entropies and S-map weights. Together these would then create a distribution of causally-filtered S-map interaction strengths capable of testing the significance of the true interaction strengths against a null hypothesis that they were equal to zero.

While we have demonstrated that causal inference can help S-maps overcome ecological multicollinearity, combining the two comes at a cost. S-maps parse variance among covarying but noninteracting species because this does a better job of accounting for systemic dynamics. Causally-filtered S-maps are averages of models with complexity bounded from above by the normal S-map model. In this way S-maps are an upper bound on the goodness-of-fit of causally-filtered S-maps. If the goal is to predict the density or abundance of a species of interest at a particular point in space and time, causally-filtered S-maps should not be used. However conservation requires explanation as well as prediction. If we wish to intervene in the decline of an endangered species, identifying the causes of its dynamics is more important than predicting the future of its dynamics.

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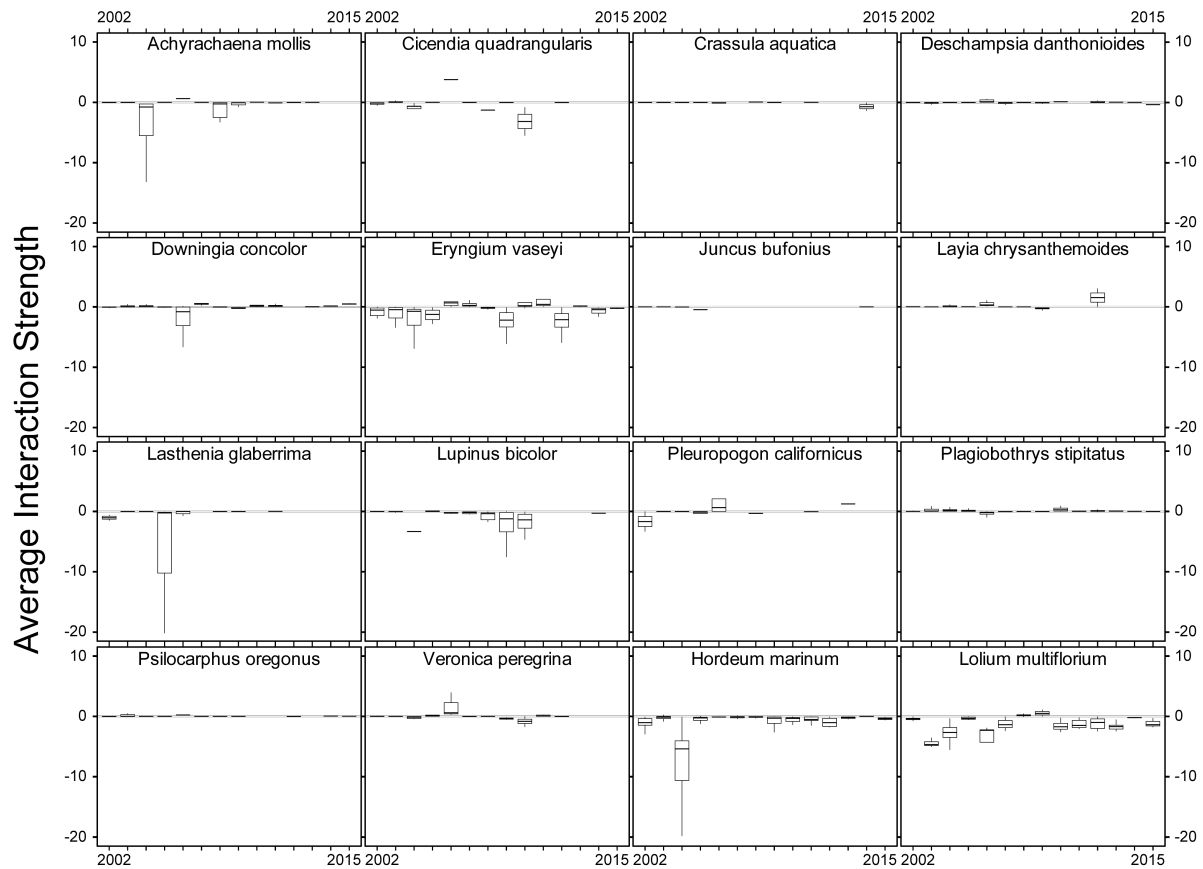
Figure C.1: Annual interspecific interactions of 14 native and 2 exotic (bottom right) vernal pool plant species with Lasthenia conjugens, measured as their per density effect on Lasthenia conjugens' annual growth rate. Boxes span interquartile ranges (IQR), with the inside bar at medians and whiskers extending to the most extreme data within $\pm 1.5 * \text{IQR}$. Missing bars indicate the species was not observed in any pool that year.
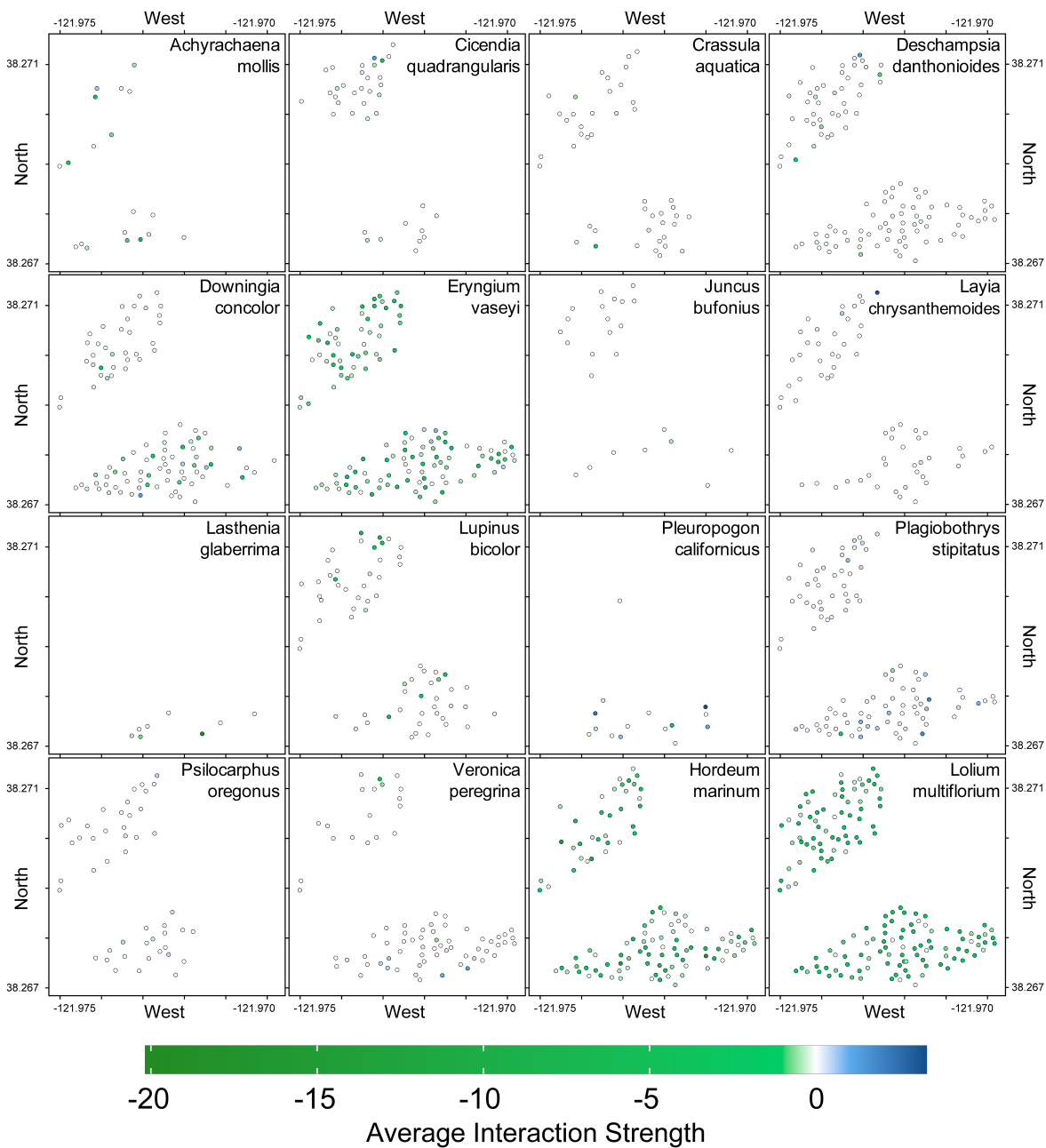
Figure C.2: Average interspecific interactions in each vernal pool of 14 native and 2 exotic (bottom right) vernal pool plant species with Lasthenia conjugens, measured as their per density effect on Lasthenia conjugens' annual growth rate. Missing pools indicate the species was not observed in between 2002 and 2015 in that pool.
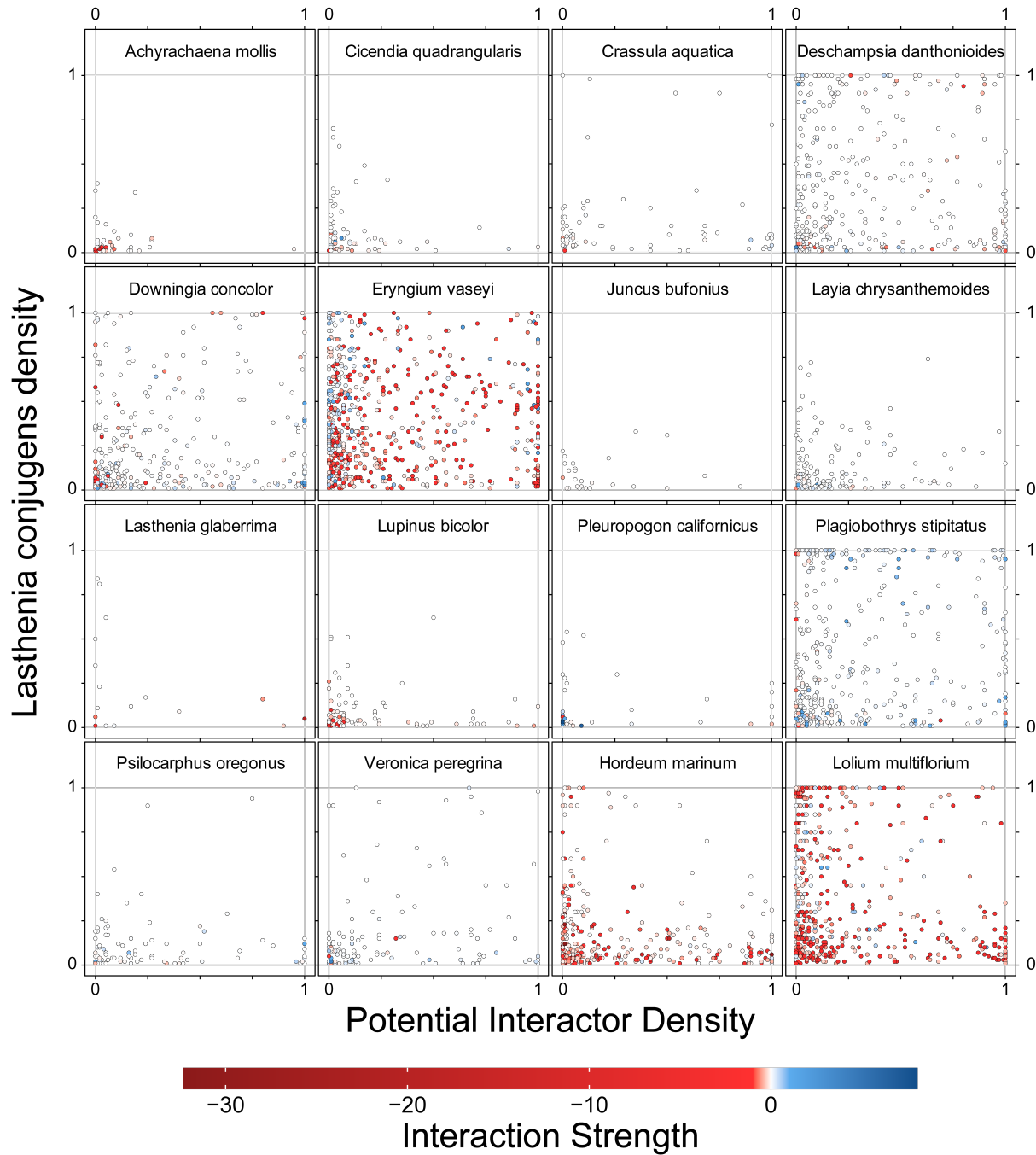
Figure C.3: Density had no effect on interspecific interactions. Each X-axis is the density of Lasthenia conjugens and each Y-axis is the density of that panel's species. Colors denote the intensity of the effect of that species on Lasthenia conjugens. Except for Erygnium vaseyi's beneficial interactions when at low density, there density had no effect on these interactions.
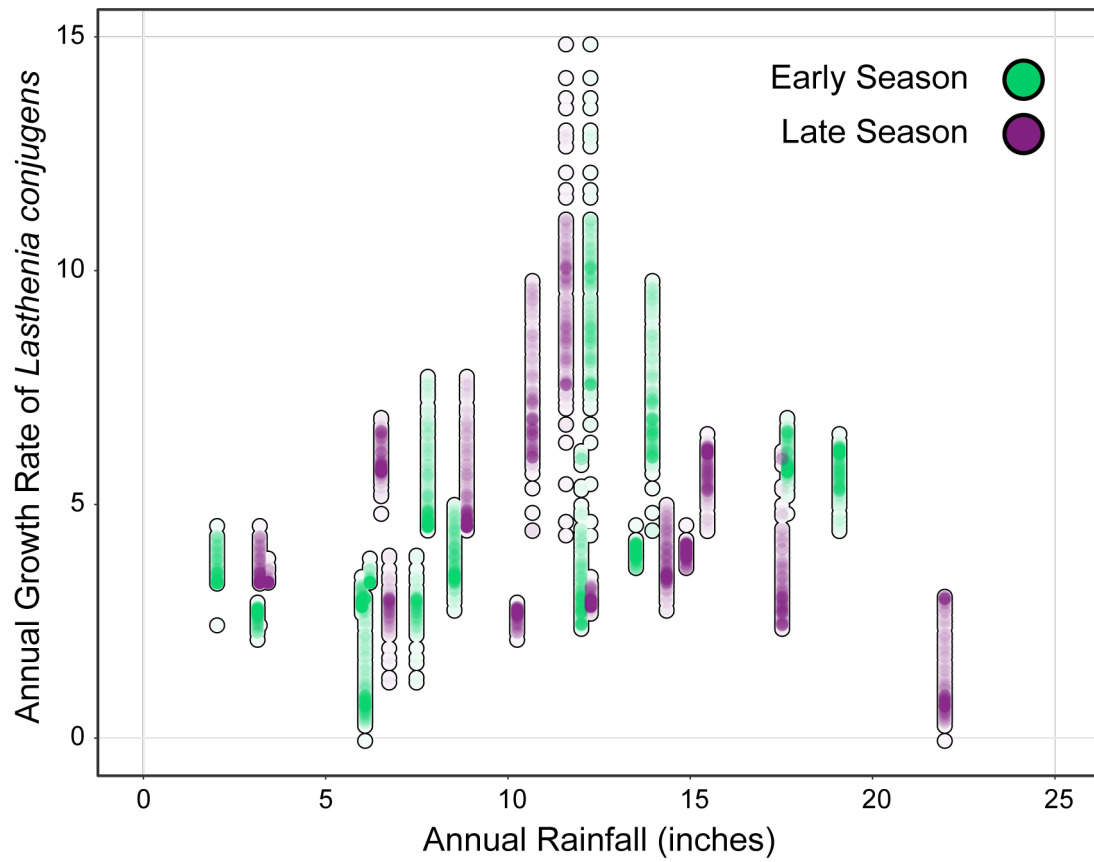
Figure C.4: Annual per density growth rates of Lasthenia conjugens as a function of early and late season precipitation. The darkness of the colors in the legend are 20 or more overlapping points.
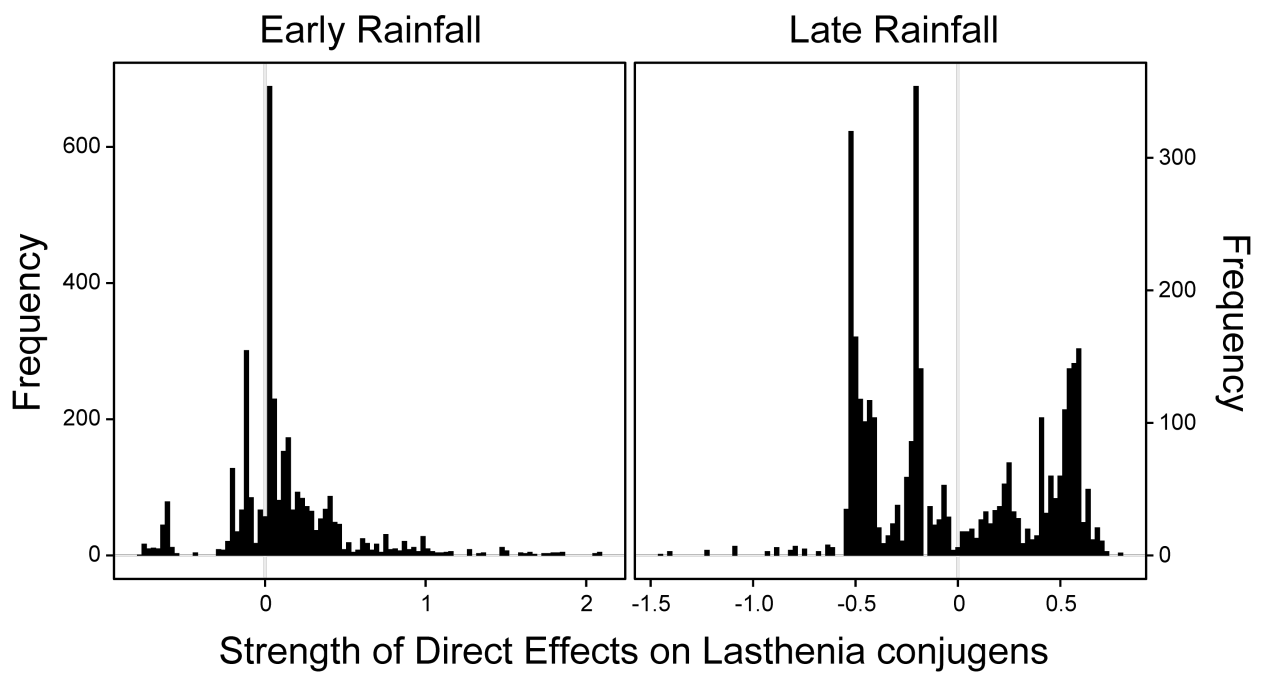
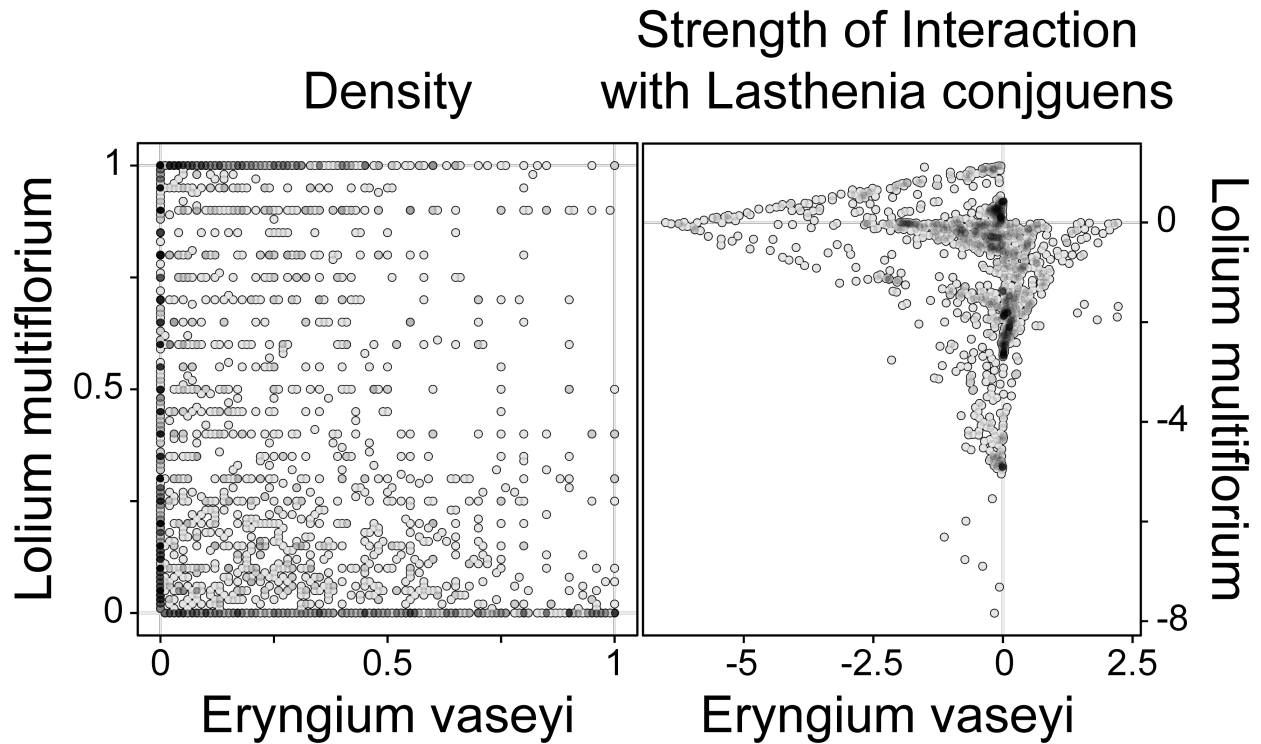Figure C.5: Distributions of direct effects of early and late rainfall on Lasthenia conjugens.

Figure C.6: The relationship between Eryngium vaseyi and Lolium multiflorium and their effects on Lasthenia conjugens. Darker regions are greater density of points, where black spots are at least 10 overlapping points. Left) If one of these species was present the other was more likely absent, seen as darker bands along the axes. The exception was when Lolium multiflorium was at a density of one, where Eryngium vaseyi was likely still present though at low densities. This reflects that Eryngium vaseyi is a perennial species. There was no relationship between the densities of these two species when both were present (interior of the left panel). Right) There was a tradeoff in the way these two species interacted with Lasthenia conjugens. As one had a great effect, the other's effect tended to weaken, reflecting there density relationship where they tended not to co-occur.
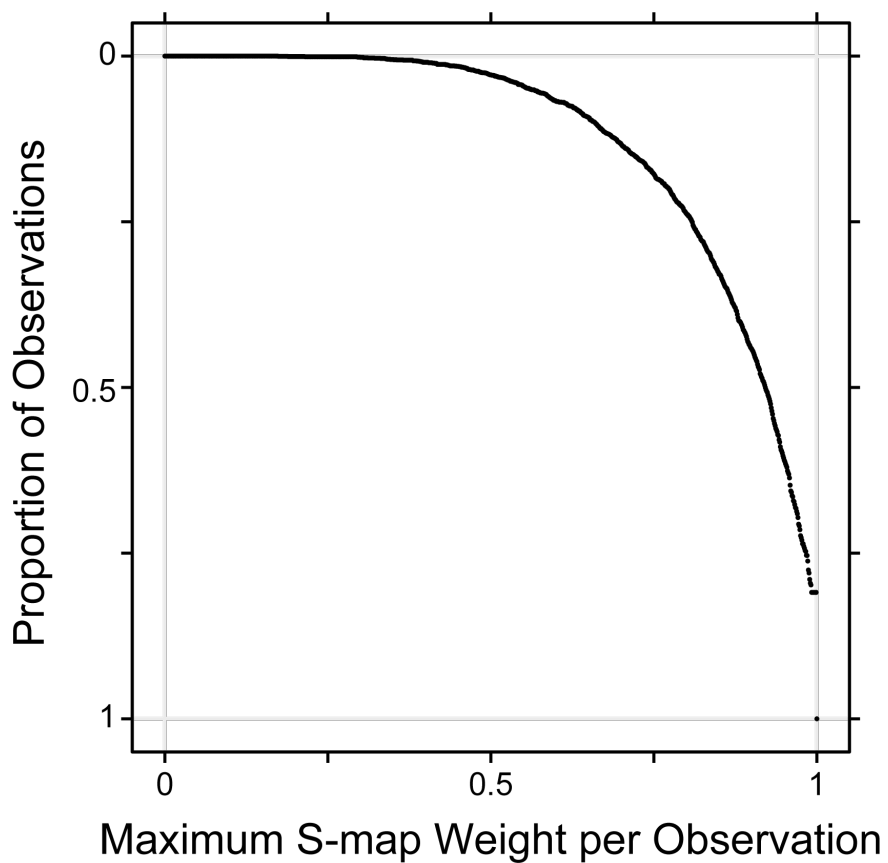
Figure C.7: The proportion of S-maps with a maximum weight of a given value. Each S-map was a multivariate regression of one observation on every other observation, and so had 3108 S-map weights (349 observations were excluded because they contained no plants). These weights which ranged between zero and one. No observations had a maximum weight of exactly one because no two observations were identical.
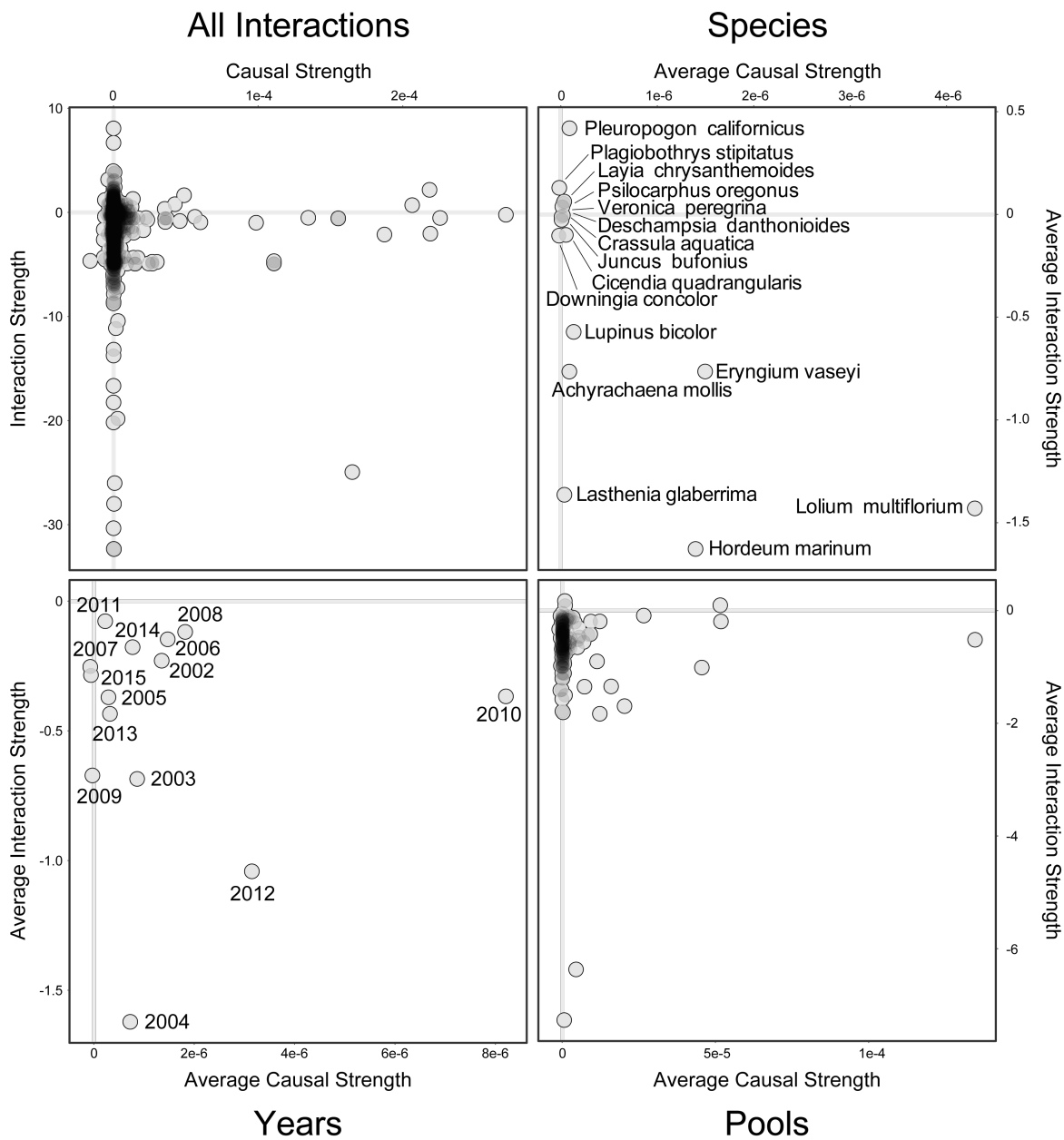
Figure C.8: The relationship between causality and interaction strength for all interactions with Lasthenia conjugens (top left) and interactions aggregated across species (top right), years (bottom left) and pools (bottom right). Causalities are bits of transferred entropy and interaction strengths are the causally-filtered S-map coefficients. Note the different scales for each panel.
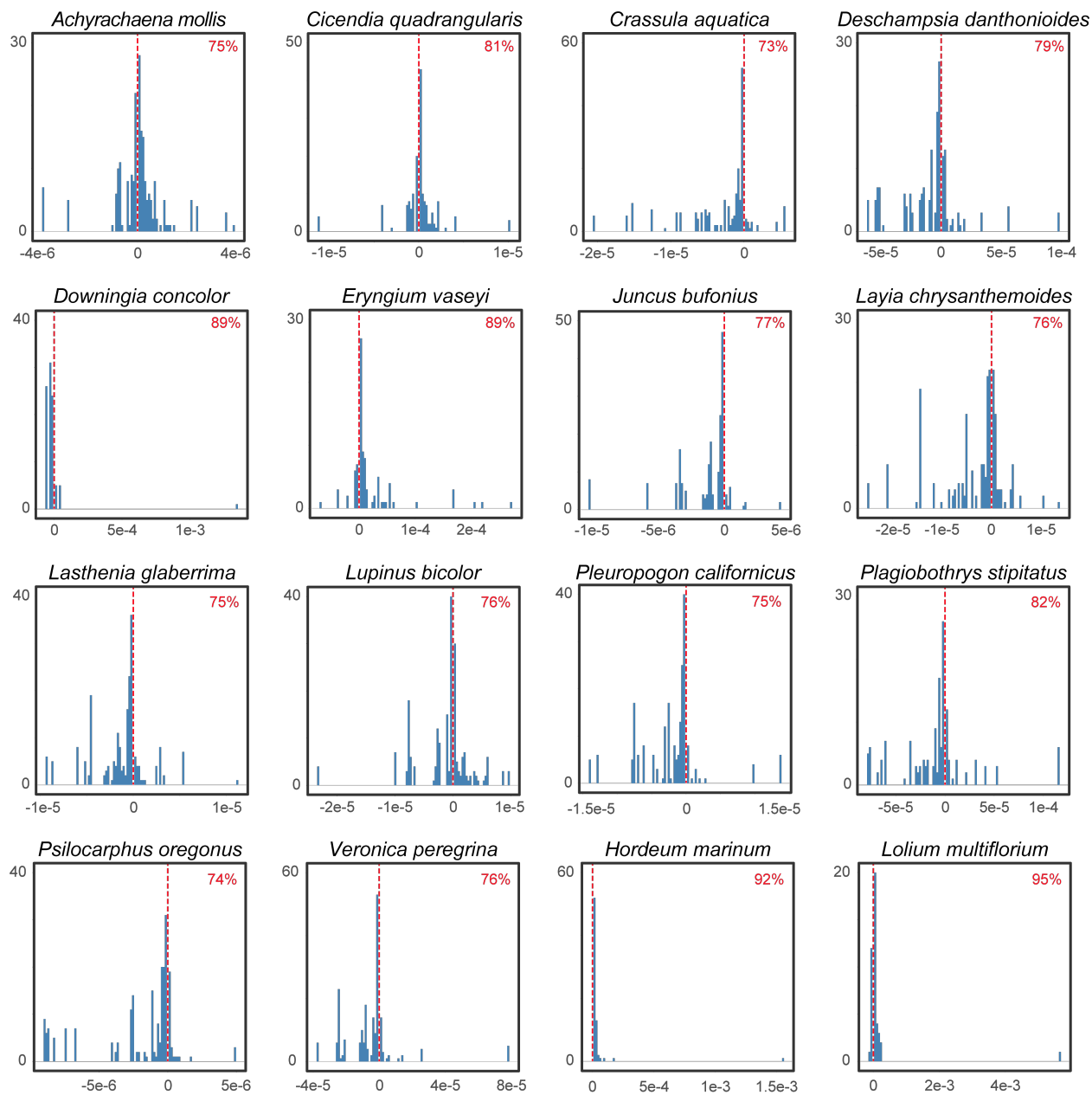
Figure C.9: Species-specific distributions of transfer entropy. Dashed red lines are where there was no transferred entropy. The relative height of these bars is listed as a percent in the upper right corner of each panel to keep the rest of the distribution visible. Note the species-specific axes.