

Investigating Invasive-Invasive Plant Relationships Through Statistical Modeling

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ABSTRACT

With global climate change, the range and distribution of invasive plant species are going to expand and change and insights into the biotic interactions which inform its range and distribution are necessary to predict the future of species ranges. Invasional meltdown is a community wide phenomenon where invasive species facilitate the establishment of other invasives until saturation. In this study, I examined if such interactions and phenomena can be investigated through modeling methods. I compared the performance of three species distribution models (SDMs), two of which have distribution data (co-occurring invasive and native plant species) incorporated as features to function as proxy variables for essential biotic interactions. I also conducted a niche overlap analysis of the two invasive study species to determine the degree and direction of their interactions; SDMs did not significantly improve with the addition of the experimental features but an analysis of feature performance measures indicate levels of competition and niche differentiation between the two species. This is further confirmed by significantly low niche overlap metrics ($p \ll 0.05$) which itself suggests intense competition. Modeling methods revealed that the two study species do not have a facilitative relationship as previously expected. Modeling methods can not just analyze invasive-invasive interaction but point to further areas of future research.

KEYWORDS

Random Forest, *Cytisus scoparius*, *Genista monspessulana*, niche overlap, invasive-invasive competition/facilitation

INTRODUCTION

As global temperatures rise, major changes to habitats are currently occurring. This environmental change can cause the range of invasive plant species to expand, creating new avenues of proliferation and possibly the degradation of native biotic communities. Invasive species can displace native species and change native community assemblages as well as reduce native biodiversity (Lortie et al. 2021). Invasive species can also restructure local mutualist networks, alter herbivory patterns and even affect parasitism (Bezemer et al. 2014). Invasive species may also co-opt native mechanisms of biodiversity preservation and use it to increase their reproductive success (Lortie et al. 2021). Although there has been some evidence how invasives may actually coexist and facilitate native communities (Rodriguez, 2006) it still does not offset the costs of treating invasive agricultural pests and weeds (Paini et al. 2016). Any insight into their spread and the interactions that inform them, become invaluable.

Biotic interactions is an important factor in forming a community's assemblage and consequently, an important factor in forming an exotic species' range. Although there have been numerous studies investigating invasive-native plant relationships, there has been limited literature on invasive-invasive interactions (Simberloff & Von Holle, 1999). There has been a diverse collection of literature investigating native-native plant facilitative effects and to a limited extent invasive-native, however facilitation can also exist between invasive species (Flory & Bauer, 2014). The extent of this facilitation varies, but it is capable of creating a positive feedback loop where the presence of one invasive species increases the likelihood of establishment of another exotic species, leading to "invasional meltdown;" a community wide change where native biota have been overtaken by established exotic species (Simberloff & Von Holle, 1999). The structure of these biotic interactions, whether facilitative or competitive, may also be highly asymmetrical (Wundrow et al. 2012), vary across an environmental gradient (Tikhonov et al. 2017) or depend on the niche overlap of the species involved (Pianka, 1974). There then needs to be a robust method to investigate the spread and range of invasive species as well as the biotic interactions that inform its distribution.

Modeling methods are a way to examine these relationships in order to assist and inform any large scale policy decisions and to indicate any avenues of future research (Riordan et al. 2018; Rodríguez et al. 2007). Although they cannot capture the full extent of the biotic and

abiotic processes which inform a species distribution, range and interactions, they are a cost effective, and efficient method of predicting species behavior (Kaky et al. 2020). Despite their versatility and predictive capabilities, many models do not incorporate essential biotic interactions or invasive-invasive interactions which could improve model performance and predictions (Pellissier et al. 2010, Giannini et al. 2013, le Roux et al. 2014, Briscoe Runquist et al. 2021).

In this study, modeling methods were used to investigate invasive-invasive interactions. Specifically, I will 1) seek to improve traditional species distribution models (SDMs) by incorporating essential biotic interactions through the introduction of distribution data of a co-occurring invasive species as a feature to the SDM and 2) investigate the degree of facilitation or competition of two invasive study species.

I hypothesized that the two chosen invasive study species would have exhibited some level of facilitation and consequently improve model performance as the invasional meltdown hypothesis anticipates a facilitative relationship between invasives.

METHODS

Study site and species

I chose three plant species from the study site as my study species. Two of which are invasive species, *Cytisus scoparius* and *Genista monspessulana* (common names Scotch broom and French broom respectively), and one native species (*Vicia americana* or American vetch). *C. scoparius* and *G. monspessulana* were chosen because of their high degree of environmental overlap and their pervasive invasiveness. Both were introduced to California as an ornamental but have since spread and naturalized all over the west coast of the United States. Both species have a Cal-IPC (California Invasive Plant Council) of High and are capable of displacing and crowding out essential native species (*Cytisus scoparius* Profile 2017; *Genista monspessulana* Profile 2017).

Although all three plants are present across the United States, the study only analyzed observations from the west coast of the United States (California, Oregon and Washington). This

is to mitigate computation cost and time while capturing the full environmental gradient of the species' range.

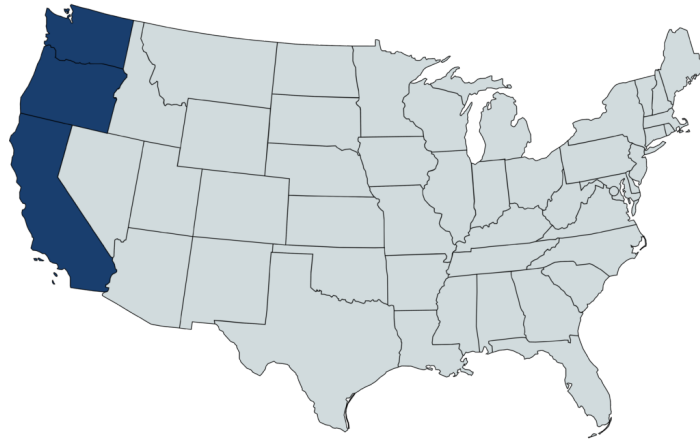


Figure 1. Study region of the experiment (CA, OR and WA).

The occurrence data for these three species were downloaded from the Global Biodiversity Information Facility (GBIF). Any observations with duplicates, coordinate issues or missing values were removed from the dataset. The resulting occurrence datasets are 10,072 observations of *C. scoparius*, 4,230 observations of *G. monspessulana* and 3,285 observations of *V. americana* (GBIF, 2021).

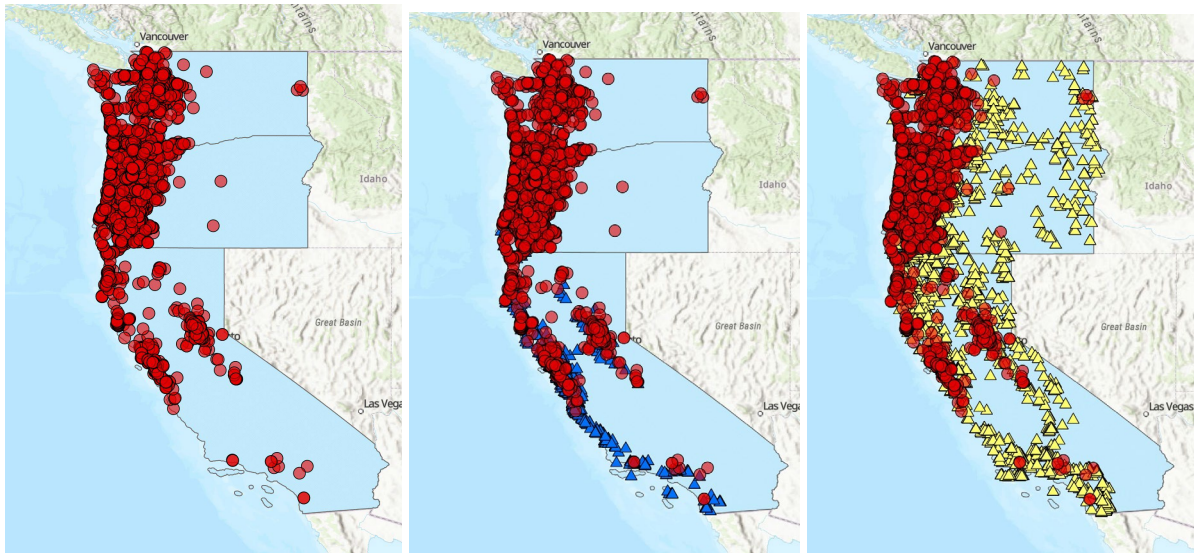


Figure 2. Occurrence records of *C. scoparius* plotted (from left to right), on its own, with *G. monspessulana* (blue triangles) and with *V. americana* (yellow triangles)

Environmental and climatic data of the study region was taken from WorldClim's 19 bioclimatic variables (Fick & Hijmans, 2017). These variables measure a variety of climatic and environmental features and have been widely used in species distribution modeling (Warren et al. 2008).

Table 1. The nineteen bioclimatic variables from WordlClim.

BIO 1	Annual mean temperature	BIO 11	Mean temp. of coldest quarter
BIO 2	Mean diurnal range	BIO 12	Annual precipitation
BIO 3	Isothermality	BIO 13	Precipitation of wettest month
BIO 4	Temperature seasonality	BIO 14	Precipitation of driest month
BIO 5	Maximum temp. of warmest month	BIO 15	Precipitation seasonality
BIO 6	Minimum temp. of coldest month	BIO 16	Precipitation of wettest quarter
BIO 7	Temperature annual range	BIO 17	Precipitation of driest quarter
BIO 8	Mean temp. of wettest quarter	BIO 18	Precipitation of warmest quarter
BIO 9	Mean temp. of driest quarter	BIO 19	Precipitation of coldest quarter
BIO 10	Mean temp. of warmest quarter		

Data preparation

I built three species distribution models (SDM), all of which were used to predict occurrences of *C. scoparius*. Because the modeling method used was a random forest classifier, an equal number of background samples to *C. scoparius* occurrence points were generated within the study region, as class imbalances can hinder the performance of random forest classifiers (Liaw & Weiner, 2002).

In order to examine the effect of the inclusion of the distribution of a co-occurring invasive species on the SDM performance of an invasive species, I made three data frames, with one for each treatment: the control treatment, the invasive treatment and the native treatment.

Each of these data frames were used to predict the distribution of *C. scoparius*. Each data frame has occurrence and background points of *C. scoparius* and the values of each of the nineteen bioclimatic variables at every occurrence/background point. The invasive treatment data frame includes occurrence data of *G. monspessulana* as a predictive feature in addition to the nineteen bioclimatic variables. The native treatment data frame includes occurrence data of *V. americana* also as a predictive feature in addition to the nineteen bioclimatic variables. This is in accordance with numerous studies that incorporate data from dominant or co-occurring species as a proxy variable for strength, degree, direction and intensity of biotic interactions (Briscoe Runquist et al. 2021, Pellissier et al. 2010, le Roux et al. 2014). Highly correlated features were not removed or decorrelated through a Principal component analysis as the purpose of the model is purely predictive and correlated features do not hinder a model's predictive capabilities (le Roux et al. 2014). The additional predictive features were downsampled into the same resolution as the nineteen bioclimatic variables. The data frames were then split (80/20) into a training and testing set. The testing set was further split into ten roughly equal folds.

All data cleaning and preparation were done in R (R Core Team 2020).

Model construction

A random forest classifier was then fitted to each of the training sets. Model construction, fitting and testing were done with the randomForest package in R (Liaw & Weiner, 2002). Each model contained a thousand trees, each built with the default parameters since random forest models are known to function well given the default arguments (Liaw & Weiner, 2002).

Model performance and testing

After the models were constructed, I tested each model with their respective test of 10 folds. The area under the receiver operating curve (AUC) for each fold was then derived, as well as a distribution of model performance of each treatment.

Creating a null distribution

To assess the significance of the degree of niche overlap of *C. scoparius* and *G. monspessulana*, a null distribution of Warren *et al.*'s (2008) niche overlap metrics of I and D were created. I created a polygon for each of the species' ranges and a hundred points were sampled from within each species' polygons. These represent virtual samples or fake observations of each species. Values from the nineteen bioclimatic variables were then extracted for each of the hundred points. Any virtual sample that fell outside of the study region or has missing values for any of the bioclimatic variables was excluded and not used for the analysis. The resulting data was then used to calculate both the I and D metric of the two invasives following Warren *et al.* (2008) using a MaxEnt model. This was repeated a hundred times to create a null distribution of both the I and D niche overlap metrics. All analysis and data preparation was done with the dismo package in R (Hijmans *et al.* 2011)

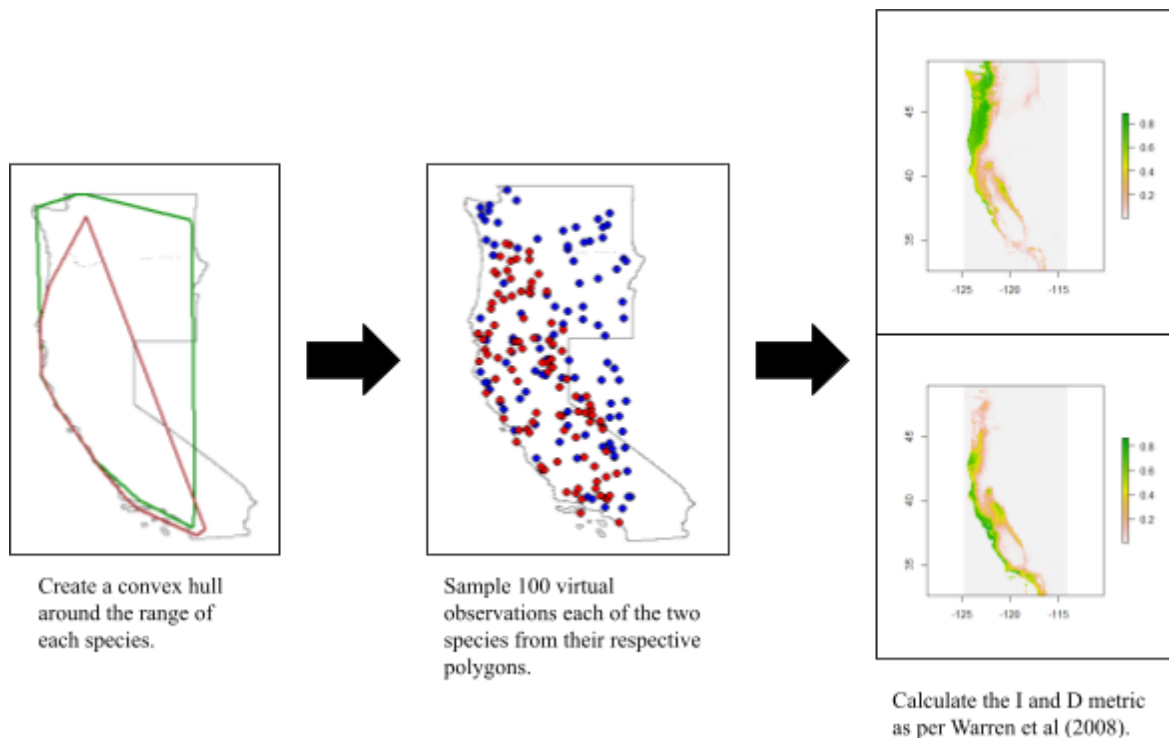


Figure 3. Construction of the null distribution of the I and D niche overlap metric for one sequence. A hundred virtual samples of *C. scoparius* (blue) were sampled within its polygon (green) and a hundred virtual samples of *G. monspessulana* (red) were sampled within its polygon (red). The heat maps on the right are MaxEnt models of *C. scoparius* (top) and *G. monspessulana* (bottom). Both are used to calculate the niche overlap metrics.

Calculating the observed niche overlap metric

Using the occurrence records of *C. scoparius* and *G. monspessulana*, I calculated the niche overlap metrics with the same methodology as described above. No convex hull was created. Instead of using virtual samples, the real observed occurrences were used. I and D were then calculated as described above.

RESULTS

SDM performance

All three models performed well. Model performance was assessed using the AUC metric, a metric which ranges from 0 to 1 and measures how well the model can discern between the two classes: presence and absence.

All three models performed far better than chance but, the model that performed the best was the native treatment (mean AUC: 0.957) followed by the control treatment (mean AUC: 0.952) and the invasive treatment (mean AUC: 0.949). This difference in performance however was not significant. A one-way ANOVA test was done and the resulting p-value was greater than 0.05 ($p = 0.245$).

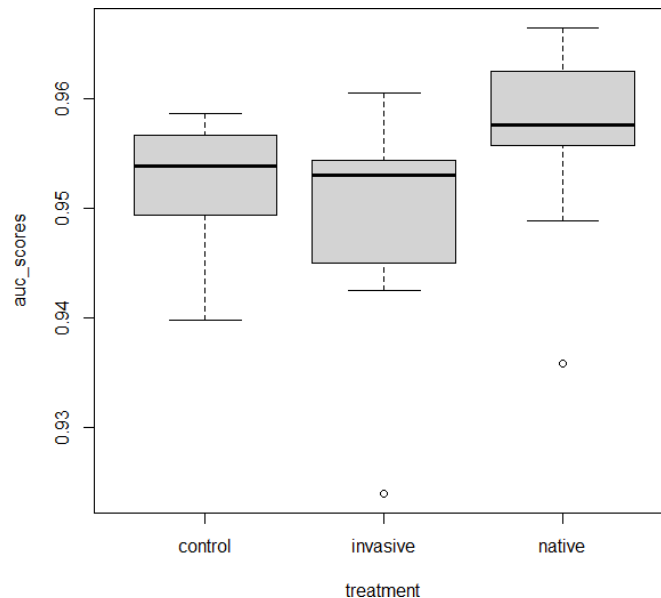


Figure 4. Average AUC scores of all three models. The native treatment received the highest average AUC score at 0.957 followed by the control treatment at an average AUC of 0.952. The invasive treatment received the lowest average AUC score at 0.949. Model performance did not differ significantly, however ($p = 0.245$).

Table 2. Variable performance measures of the invasive and native treatment. Mean decrease accuracy measures of the invasive treatment (columns 1-2) and the native treatment (columns 2-4). Mean decrease GINI measures of the invasive treatment (columns 3-4) and the native treatment (columns 5-8).

<i>G. monspessu lana</i>	37.7	<i>V. americana</i>	24.2	<i>G. monspessu lana</i>	46.3	<i>V. americana</i>	17.9
BIO 1	51.7	BIO 1	49.5	BIO 1	179.5	BIO 1	186.9
BIO 2	50.4	BIO 2	50.0	BIO 2	140.7	BIO 2	151.7
BIO 3	54.0	BIO 3	55.5	BIO 3	315.1	BIO 3	332.1
BIO 4	44.8	BIO 4	45.2	BIO 4	854.3	BIO 4	729.2
BIO 5	68.8	BIO 5	65.0	BIO 5	574.0	BIO 5	590.8
BIO 6	52.3	BIO 6	51.7	BIO 6	144.2	BIO 6	141.9
BIO 7	41.8	BIO 7	44.3	BIO 7	952.1	BIO 7	849.2
BIO 8	39.7	BIO 8	41.2	BIO 8	433.9	BIO 8	465.5
BIO 9	37.9	BIO 9	38.4	BIO 9	241.9	BIO 9	259.1
BIO 10	40.1	BIO 10	41.5	BIO 10	355.6	BIO 10	306.4
BIO 11	45.4	BIO 11	43.5	BIO 11	750.8	BIO 11	751.8
BIO 12	76.1	BIO 12	74.8	BIO 12	258.7	BIO 12	250.9
BIO 13	50.3	BIO 13	50.5	BIO 13	279.6	BIO 13	281.2
BIO 14	42.5	BIO 14	43.6	BIO 14	513.5	BIO 14	669.1
BIO 15	47.9	BIO 15	47.4	BIO 15	772.9	BIO 15	794.1
BIO 16	76.8	BIO 16	78.1	BIO 16	156.5	BIO 16	162.0
BIO 17	61.7	BIO 17	60.6	BIO 17	286.2	BIO 17	316.1
BIO 18	56.0	BIO 18	55.3	BIO 18	276.6	BIO 18	263.5
BIO 19	57.1	BIO 19	59.1	BIO 19	382.9	BIO 19	396.6

Niche overlap

C. scoparius and *G. monspessulana* share a significantly low degree of niche overlap across both the I and D metric. When comparing the observed niche overlap metric of the two invasive species against the null distribution, the observed metric does not overlap with the null distribution. The effective p-value is $\ll 0.05$, the two invasive study species have a significantly low niche overlap metric across both D and I. *C. scoparius* and *G. monspessulana* have a D and I statistic of 0.506 and 0.782 respectively. The null distribution averages a D metric of 0.704 and an I metric of 0.929 with a standard deviation of 0.051 and 0.018 respectively.

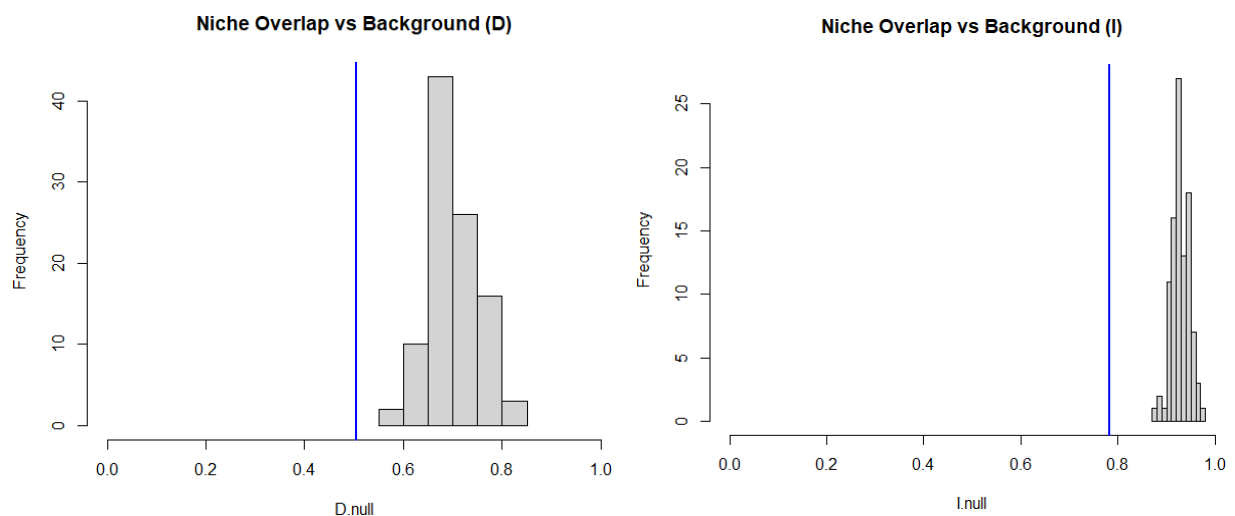


Figure 5. The observed niche overlap metric (blue line) plotted against the null distribution.

DISCUSSION

SDM treatments: control, invasive, native

Comparing SDM performances across treatments

All three models reached AUC scores above 0.5 which is the threshold for a decent model as an AUC of 0.5 indicates that the model is making random predictions for both classes. In fact all of the models reached an average AUC of ~ 0.9 . Despite the high performance of all three models, the difference in performance across models was not significant ($p = 0.245$). Incorporating distribution data of a co-occurring plant, whether invasive or native, does not

improve SDM performance.

The results did not fit my hypothesis. By incorporating distribution data of co-occurring species, I hoped to improve model performance by including the intensity, and class of biotic interactions through proxy variables (le Roux et al. 2014). Additionally, the effects of the invasional meltdown hypothesis would have anticipated an improved performance of the invasive treatment as it captures the theoretical facilitative effects that invasive species exert on each other.

Inadequate data, environmental variability and different performance measures.

Possible reasons for the lack of model improvement is likely due to lack of data quality, the environmental variability of the study site and the testing metric for model performance.

Occurrence data of all three species were derived from GBIF, however similar studies used a combination of publicly available data and field surveys of the study sites (Briscoe Runquist et al. 2021; le Roux et al. 2014; Pellissier et al. 2010). Because of this methodology, the data is more robust and more representative of the actual distribution and range of the study species. Briscoe Runquist *et al.* (2021) conducted an additional layer of data analysis to increase data reliability. The study performed a Joint Species Distribution Model to determine any co-occurring species with a high degree of correlation. Inputting data of a co-occurring species may be insufficient as co-occurring does not equate to correlation.

Additionally, the extent and the relationship between *C. scoparius* and *G. monspessulana* or *V. americana* may vary across different environmental gradients. Interspecific interactions have been shown to vary across environments (Tikhonov et al. 2017) and le Roux *et al.* (2014) have demonstrated that model performance differed across different environments as well as across dominant plant densities. Model performance then could change if the scale was limited to a single homogenous region.

Lastly, model performance metrics may be inadequate when quantifying the SDM performances of invasive species. AUC has shown to be a poor measure of model performance (Lobo et al. 2008); it equally weighs omission and commission errors which can prove to be misleading for presence-only modeling methods.

Niche overlap

Invasive-invasive competition.

C. scoparius and *G. monspessulana* have a significantly low overlap metric that is indicative of a high degree of competition (Pianka, 1974). Across both D and I, the two invasive plant species are consistently significantly lower than expected by chance. This competitive relationship goes against the invasional meltdown hypothesis as detailed by Simberloff & Von Holle (1999). According to the hypothesis, these two invasive species should be exhibiting some level of facilitation, whether it is reciprocal or asymmetric.

However, Simberloff (2006) clarified the hypothesis and stated that instances of a full scale community level change outlined by the hypothesis has been rare. There have been numerous examples of invasive-invasive facilitation, but rarely to the extent where entire communities would be replaced by exotics; facilitation among invasives seem to have a threshold.

Both *G. monspessulana* and *C. scoparius* have long been established in the west coast of the U.S. and may have since long passed the threshold for invasional meltdown to occur. Such phenomena may have played a more important role during the initial stages of invasion as *C. scoparius* and *G. monspessulana* established themselves in California during the 1800s (*Cytisus scoparius*; Species: *Genista monspessulana*).

Competition in SDMs

Model performance versus feature performance.

Variable performance metrics were and should be interpreted cautiously if a number of the features used in the model are highly correlated - such metrics may be misleading and not representative of the feature's actual performance. However, there is a discrepancy between model performance and feature performance that might be worthwhile to examine.

Although not significant, the native treatment performed the best out of all three treatments. All three treatments are identical, except for the addition of the invasive feature (distribution data of *G. monspessulana*) in one model and the addition of the native feature

(distribution data of *V. americana*) in the other. Because the native model performed the best, it would be expected that most of the improvement is due to the inclusion of the native feature but such is not the case. When comparing across mean decrease in accuracy and mean decrease GINI, the native feature consistently performed the worst out of all the features.

Hyperparameter tuning, niche differentiation and significance levels

Because of the consistently low performance scores of the native feature, the random forest algorithm may be effectively limiting the number of random features it evaluates at every split. The inclusion of the native feature may be inadvertently tuning a hyperparameter and essentially improving model performance despite the presence of a low performing feature.

Additionally, *V. americana* could possibly be interspersed within the range of *C. scoparius* at a finer scale than *G. monspessulana*. The difference between the mean decrease GINI of *G. monspessulana* and *V. americana* is larger than the difference between the mean decrease in accuracy of *G. monspessulana* and *V. americana* - the invasive feature outperforms the native feature in the mean decrease GINI and produces purer nodes. This indicates that *G. monspessulana* is better at discriminating presences and absences of *C. scoparius* than *V. americana*, suggesting that the boundaries between populations of the two invasives are more distinct than the native and the invasive. Competitive interactions may be preventing the diffusion of such clear boundaries.

It may also imply a huge differentiation in the niche of both invasive species. The niche of the two species are so distinct that it can produce purer splits. Either possibility is supported by the significantly low measure of niche overlap of *C. scoparius* and *G. monspessulana*; it is both an indication of a very clear differentiation of resource use (niche) between the two species and an indication of a high degree of competition.

Limitations and Future Directions

It is important to emphasize however that the difference in model performance is not significant so any form of improvement could just be the result of random chance and feature performance measures might not present the full picture of a feature's predictive power

especially if features are correlated. Data quality could definitely be improved by conducting field samples to increase reliability and robustness of the occurrence data. Additional preliminary analysis of data can also benefit the study by improving study species selection.

Lastly, an experimental confirmation of these findings would greatly benefit the study. Modeling methods can never capture the full degree of interactions and factors present at the field and so an experimental design can advance the study.

Conclusion

Incorporating biotic interactions into SDMs are essential however such features need to be incorporated into the model through more statistically robust means. Additionally, because of the high degree of competition between *C. scoparius* and *G. monspessulana*, any policy which advocates for the removal of one should be scrutinized and examined as the removal of one could lead to the expansion of the other.

Invasive-invasive plant species interactions, although often overlooked, are an essential aspect of plant community assembly processes and should be incorporated into more modeling methods. As global climate continually changes, we can expect the spread of more and more exotic species and invasive-invasive interactions can become invaluable tools to manage and mitigate the effects of alien establishment. Invasive-native relationships are well represented in the literature while studies on invasive-invasive relationships are lacking. This project shows how modeling methods can shed light on invasive-invasive interactions and point to potential areas of research.

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