

## Improving range shift predictions: enhancing the power of traits

**Running Title:** Improved range shift predictions via traits.

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### Abstract

Establishing criteria to enable prediction of species' range shifts under environmental change is a motivator for many modern ecological studies, and the use of functional traits as a source of  
15 these general criteria has been studied extensively. In many studies, traits emerge as significant but weak predictors of species' range shifts across recent climate change. These studies assume linearity in the relationship between a trait and its function, while detailed empirical work often reveals unimodal relationships, thresholds, and other nonlinearities in many trait-function relationships. We hypothesize that the use of linear modeling approaches fails to capture these  
20 nonlinearities and therefore may be under-powering traits to predict range shifts. We evaluate the predictive performance of four different modeling approaches that can capture nonlinear relationships (ridge-regularized linear regression, ridge-regularized kernel regression, support vector regression, and random forests). We validate our models using four multi-decadal range shift datasets in plants, small mammals, and pelagic marine species. We show that nonlinear  
25 approaches perform better than least-squares linear modeling in reproducing historical range shifts. In addition, using novel model observation and interrogation techniques, we identify trait classes (e.g. dispersal- or diet-related traits) that are primary drivers of model predictions, which is consistent with expectation. These results highlight the effectiveness of new approaches for

leveraging species traits as valuable predictors of range shifts given global environmental  
30 change, which can meaningfully inform decision making and species vulnerability analyses.

**Keywords:** traits, range shifts, nonlinear modeling, ecological forecasting, global change  
responses, XXXX XXXX

## 35 **Introduction**

Species have been responding to recent climate change by tracking their environment in space or  
time, adapting or acclimating, or facing declines (Parmesan, 2006), but we are largely unable to  
predict how particular species will respond (Maguire *et al.*, 2015). Extensive documentation of  
shifts in distribution and seasonal timing (phenology) reveal that responses vary among species  
40 markedly in direction and extent (Rapacciuolo *et al.*, 2014). Detailed empirical studies often  
succeed in identifying functional traits that govern climate change responses (e.g., Adrian *et al.*,  
2006) and consequently functional ecology has been rapidly gaining prominence in climate  
change ecology (Buckley & Kingsolver, 2013). However, attempts to use traits to predict the  
relative magnitude of responses among species generally identify traits that are significant, but  
45 weak, predictors of climate change responses (Estrada *et al.*, 2016; MacLean & Beissinger,  
2017). Across studies, species traits were found to account for ~16% of the among species  
variation in range shifts and ~42% of the among species variation in phenological shifts  
(Buckley & Kingsolver, 2013). How can we close the discrepancy between traits predicting  
responses well in detailed studies but poorly in broad studies? What statistical techniques will  
50 allow us to generalize the importance of traits in mediating climate change responses?

Addressing such questions is imperative for anticipating and adapting to the biological impacts of climate change. Indeed, traits are already being used to predict species' sensitivity to climate change in vulnerability frameworks (Williams *et al.*, 2008; Foden *et al.*, 2013; Pacifici *et al.*, 2015). However, the frameworks remain largely untested. Moreover, the traits included in vulnerability analyses differ sufficiently that different frameworks predict dramatically different rankings of vulnerability (Wheatley *et al.*, 2017). Improving the ability of traits to predict climate change responses is necessary for robust vulnerability analyses.

Most attempts to use species' traits to predict the magnitude of their climate change responses rely on linear regression (Buckley & Kingsolver, 2013; MacLean & Beissinger, 2017), yet detailed empirical studies often reveal non-linear relationships between traits and their function (Stenseth & Mysterud, 2002). Unimodal relationships and thresholds are common. For example, extreme diet specialization may drive a species to track the range shift of a food item (Altermatt, 2010; Diamond *et al.*, 2011), but reducing diet specialization only slightly may alleviate the need for a species to track its food. Diet generalization could facilitate species moving to capitalize on newly climatically suitable habitat, yielding a unimodal relationship between diet specialization and the magnitude of range shifts. Likewise, low dispersal ability may prevent a species from tracking its environmental niche (Schloss *et al.*, 2012), but the threshold of dispersal ability that allows species to track their niche may be relatively low. Can statistical techniques that allow for non-linear relationships between traits and species' responses improve our predictive ability?

The universe of modeling techniques is vast, and offers ecologists a wealth of tools to assess whether these nonlinear interactions between traits and range shifts can predict future responses. Standard approaches to capture variable interactions and nonlinearities in linear regressions (such as the explicit inclusion of interacting variables or polynomial expansion) rely on prior knowledge or model selection techniques to determine which variables to select. Other model types, such as machine learning approaches that optimize model parameters, are better suited than brute-force techniques to capture functional relationships among variables. These models, while offering statistical-robustness and efficiency, can be opaque and rarely afford clear coefficients to inspect when assessing the model's learned correlations. However, developments in the field of machine learning offer new approaches for inspecting model performance and predictions.

Limited computational background among ecologists has restricted application of the methods despite the complex, interacting relationships inherent in many ecological studies (Olden *et al.*, 2008). Some biological domains (e.g. the identification of novel zoonotic disease reservoirs (Han *et al.*, 2015)) have showcased the potential of advanced machine learning, and methods like neural networks (Olden *et al.*, 2008), boosted regression trees (Elith *et al.*, 2008), and random forest classifiers (Cutler *et al.*, 2007) are gaining traction in applications such as species distribution modelling. Largely, however, these methods have not seen wide use in capturing non-linear biological responses such as organismal responses to climate change.

Here we assess whether machine learning-based models can better use species' traits to predict the magnitude and direction of range shifts observed in response to recent climate change. First,

we consider whether several models which are able to capture nonlinear relationships can outperform linear models in their predictive ability. Second, we assess the trustworthiness of these predictions using recent developments in model interpretability techniques: does the basis for a model's predictions represent rigorous and supported ecological theory? The use of a novel model inspection approach addresses reasonable concerns about the "black box" nature of many machine learning-based models by offering a more detailed look at the model predictions. We assess these aspects using four datasets encompassing a broad taxonomic range. The number of included species ranges from 20 to 176 and range shifts were observed over time spans ranging from 30 to 100+ years. Each dataset consists of a list of focal species, associated species-level traits, and a range shift metric. We examine (1) whether non-linear methods can improve predictive ability of traits compared to linear methods, (2) whether the novel methods identify important traits consistent with significant results from other studies, and (3) whether the directionality of the modeled effect of traits is consistent across model types.

## **Materials and Methods**

We describe the nonlinear modeling approaches, a framework for interpreting model predictions, and the assembly of range shift and trait data to determine whether traits can play a more powerful role in predicting ecological responses to climate change.

### **Modeling Approach**

We applied three classes of learning algorithms: regularized linear regression, kernel-based regression, and tree-based regression. Regularization is a modification to traditional generalized linear regression which limits the complexity of the learned model to avoid overfitting to the data (Hastie *et al.*, 2009). Several types of regularization exist; we chose to use a "ridge"-regularized

120 linear model, which imposes a penalty on the magnitude of each learned coefficient. The cumulative effect of this regularization procedure is a set of coefficients which both minimize prediction error on the training data and prevent overfitting. These coefficients can be interpreted explicitly as with ordinary least squares regression.

125 While regularization reduces overfitting when compared to a standard least-squares linear fit, regularized linear models are still not able to capture nonlinearities among or interactions between predictive variables. To remedy this, we employ two additional classes of models: kernel-based regression and tree-based regression. A “kernel” is a function which projects a set of input data, often into a high-dimensional space, to allow for the linear “separability” of the data for the purposes of classification or regression (Hastie *et al.*, 2009). The Kernel Ridge method employed herein uses a radial basis function (or squared exponential) kernel applied to the training data and fits a ridge-regularized linear model to this transformed input. As a result of this transformation the learned coefficients, while regularized, are not immediately interpretable. We also evaluate a kernel-based technique known as a support vector machine (SVM). This popular learning method can be formulated for regression, is robust to outliers, and can capture nonlinearities and variable interactions through a similar radial basis function kernel as in the Kernel Ridge approach. Similarly to the Kernel Ridge method, the SVM regressor does not have interpretable coefficients. Finally we train a random forest regression algorithm to evaluate the performance of tree-based methods. All of these models are implemented using in the Python programming language using the scikit-learn software package (Pedregosa *et al.*, 2011). All code for this project is available on GitHub in Jupyter notebooks, a “literate programming” format

which combines text and executable code viewable in a web browser. The code is located at [http://github.com/huckleylab/cc\\_traits](http://github.com/huckleylab/cc_traits).

145 For comparison to the original analyses, we train an ordinary least squares regression model, which assumes linear relationships and no variable interaction. While the original analyses were mostly conducted in a single-variable framework (that is, to assess the effect size of  $M$  different potential predictive variables  $M$  models were trained, each model containing only 1 variable), we include all variables in single analyses to enable the models to capture variable interactions and  
150 to follow a common predictive modeling paradigm.

### Evaluation

We use data subsets for performance evaluation. To assess the predictive performance of our models we employ a  $k$ -fold cross-validation scheme (Hastie et al. 2009) combined with a squared  
155 error loss function. This cross-validation technique estimates expected prediction error by randomly partitioning data points into  $k = 10$  subsets, each with  $N/k$  members;  $k - 1$  subsets are used to fit the model (the “training set”), reserving one subset for testing model performance. Each of the  $k$  subsets is used exactly once for evaluation. A mean squared error (MSE) loss is then computed for the model prediction of range shift magnitude in the reserved test data, which  
160 is the sum of squared differences between predicted and actual range shift magnitude over all data in the testing set. This process is repeated  $k$  times and a mean statistic is computed across the  $k$  MSE values that result (known as a “cross-validation mean”). The same cross-validation mean approach is used to compute average variable importance values to evaluate model drivers, described below. In these experiments we choose  $k = 10$  (Hastie et al. 2009).

### Model Interpretation

The core of any basic regression analysis is typically an inspection of the significance of the coefficients of a fitted model. However, the kernel methods employed herein (Kernel Ridge, SVM) do not expose any interpretable coefficients. To address this, we utilize the Shapley additive feature value method, proposed in Lundberg and Lee (2017). Shapley values are computed for each variable by treating the explanation of a given model's prediction as a model in and of itself—values are computed by training an additive method derived from cooperative game theory to learn each variable's contribution to a model's prediction. Explanations are generated from each prediction in the model training set to identify the most important variables during training, and are averaged for each feature across all training examples to generate a whole-model feature importance scale. We perform this procedure for each of the training sets generated by the cross-validation scheme described above to compute average feature importance values. To compare the learning techniques, we use either mean regression coefficients (for OLS and Ridge regression), mean Shapley variable importance values (Kernel Ridge and SVM), or mean Gini variable importance values (Random Forest; Brieman, 2011) to rank all variables such that each feature has an importance ranking for each of the several regression methods. All means are  $k$ -fold cross-validated means.

### Trait and Range Shift Data

We evaluate our approach independently by replicating analysis across four datasets that (1) repeated historical surveys or conducted continuous surveys along latitudinal or elevational gradients to quantify shifts in northern or upper elevation range boundaries over at least three

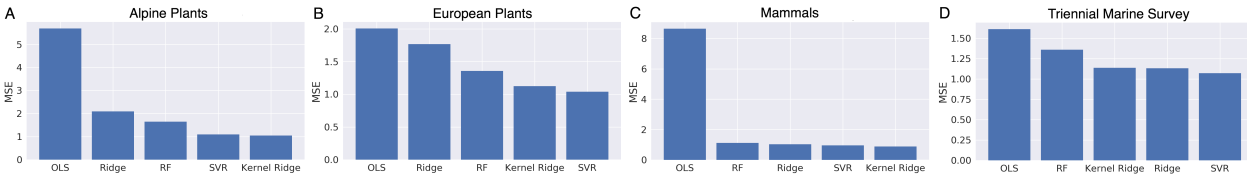


decades of change and (2) included all surveyed species (i.e. rather than including only species that shifted significantly). The first two data sets are those used by Angert et al. (2011) to assess the predictive power of traits. These datasets supplement trait data in datasets of elevational range shifts for Swiss alpine plants (Holzinger et al. (2008),  $N = 139$ ) and for Western North American small mammals (Moritz et al (2008)). A third database from Rumpf et al. (2018) consists of elevational range shifts for European montane plants coupled with trait data derived from the TRY Plant Trait Database (Kattge et al., 2011; <https://www.try-db.org>) and other databases. The fourth database was created by pairing estimates of range shifts from coastal North American marine fish surveys (Pinsky et al., 2013) with functional trait data in Fishbase (<https://www.fishbase.org>, Froese and Pauly, 2018). We remove samples which are missing any features, one-hot encode categorical features (i.e., generate one boolean column for each category), and normalize/center the numeric features to have zero mean and unit norm. After this processing the Swiss plants dataset contains  $N = 20$  species and  $d = 38$  features; the Yosemite mammal dataset contains  $N = 28$  species and  $d = 19$  features; the marine fish dataset contains  $N = 76$  species and  $d = 17$  features; the European plants dataset contains  $N = 176$  species and  $d = 18$  features.

## Results

We find that the machine learning approaches universally improve predictive performance over an ordinary least squares (OLS) model baseline. For two datasets (Swiss alpine plants and Western NA mammals), the four machine learning approaches perform substantially better than the OLS models but similarly to each other. For the other two datasets (European montane plants

and coastal fish), the performance advantages of the machine learning approaches are less substantial and the four machine learning approaches differ more in their performance. Support Vector Regression (SVR) and Kernel Ridge emerge as the most performant methods across datasets (**Figure 1**), with an average reduction of MSE of 67.6% and 67.5% relative to OLS, respectively. We focus on results from the Swiss alpine plants dataset (Holzinger et al. (2008) and Angert et al. (2011)) to demonstrate findings which are recapitulated across the other datasets in this study.

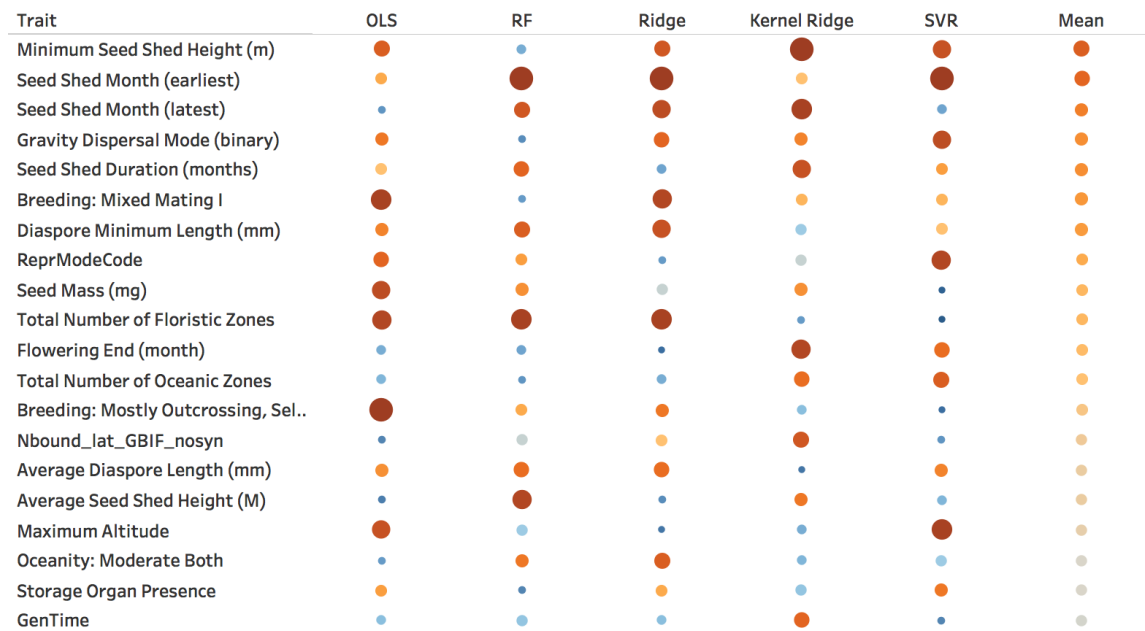


**Figure 1:** The four machine learning approaches reduce the mean squared error (MSE, 10-fold cross-validation) of range shift predictions below the MSE of the standard linear regression approach (OLS: ordinary least squares) across all four datasets (A-D). Support Vector Regression (SVR) and Kernel Ridge models exhibit stronger performance than ridge regularized linear (Ridge) or Random Forest (RF) models across the datasets.

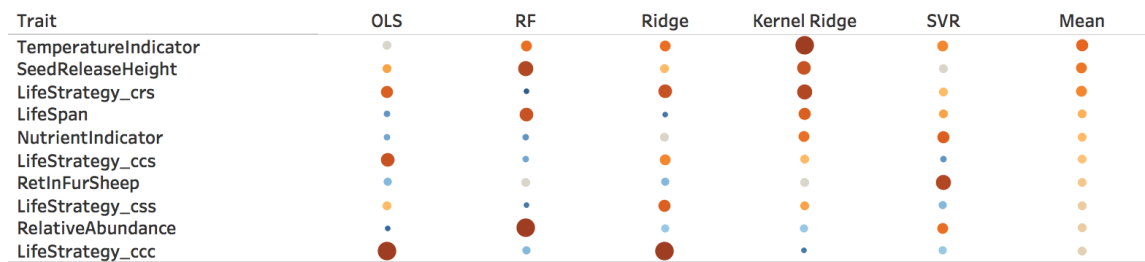
In addition to reducing MSE, the machine learning models select traits important to predicting range shifts that are expected given previous work and ecological theory. The most performant models for these data (SVR and Kernel Ridge, lowest MSE: **Figure 1, panel B**) identify dispersal-related traits as the most important variables in predicting range shift magnitude (**Figure 2, top panel, left axis**), which is consistent with our expectation and prior work. In the original analysis of the European Plants data (Rumpf et al., 2018) the “TemperatureIndicator” variable was a primary predictor of range shifts; our models selected the same variable as most important (**Figure 2, panel B, left axis**). The previous Western NA mammal analysis (Angert et

al. 2011) identified altitudinal limit as a significant predictor and longevity as a relatively strong, but non-significant, predictor. Our models select those two variables as the most important  
235 predictors. Previous analysis (Angert et al. 2011) of the Swiss alpine plants did not identify strong predictors, but did suggest- consistent with our analysis- that dispersal ability influence the magnitude of range shifts.

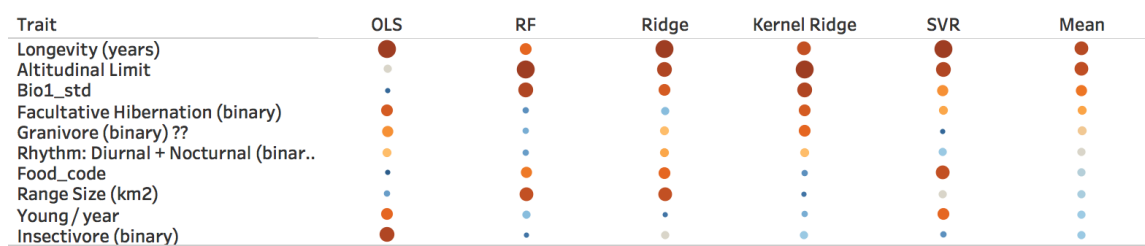
## A – Alpine Plants



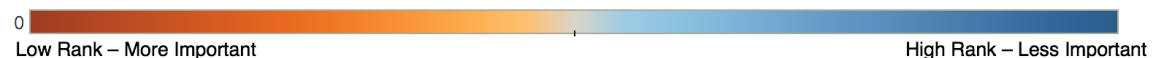
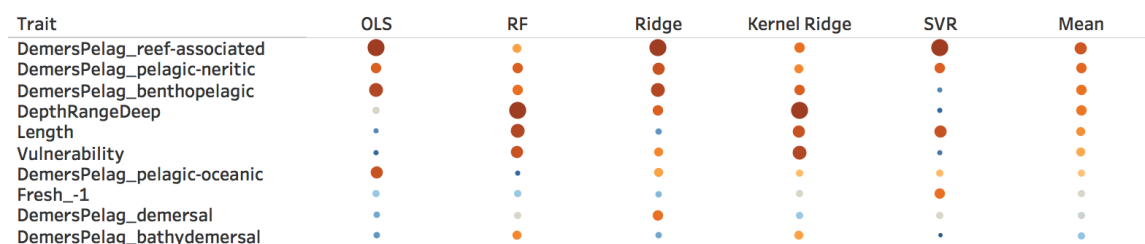
## B – European Plants



## C – Mammals



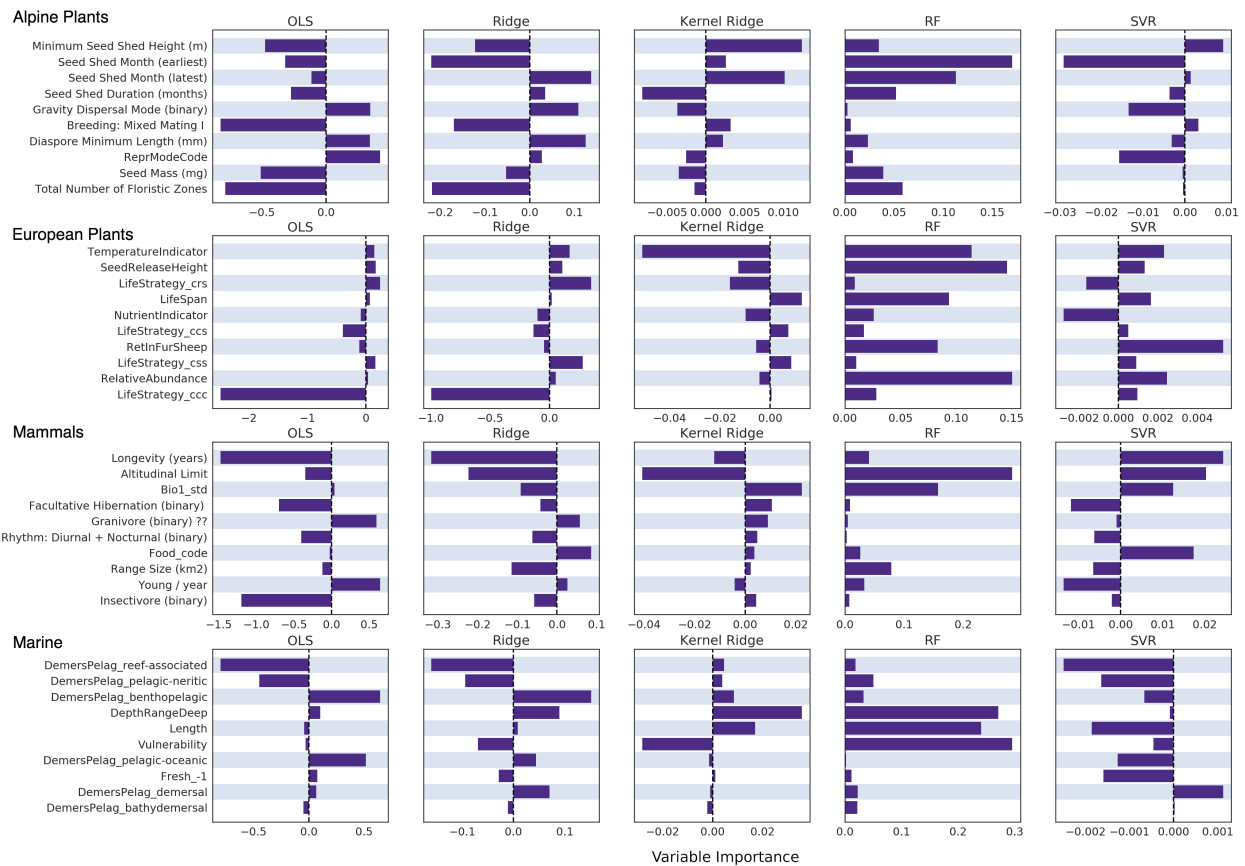
## D – Triennial Marine Survey



**Figure 2:** The model approaches select similar traits as important (larger and red = more important) for predicting range shifts across datasets. Traits are listed in order of decreasing mean importance (increasing mean rank, right column) across all methods for each dataset (panels). Model abbreviations are as in Figure 1.

The models employed in this analysis also demonstrate cross-model consistency in identifying trait drivers of range shifts (**Figure 2, large red marks at top of panels**). In other words, separate models tend to agree on trait rank, especially in the top 5 traits, suggesting a common effect despite significantly different modeling methodologies (and evaluation strategies).

Finally, for models that assign directionality to a modeled effect (all models except Random Forest), models also tend to agree in the directionality of how traits influence range shifts (**Figure 3**). It is important to note that these measures of variable contribution are computed in distinct ways depending on the modeling methodology. Using these heterogeneous metrics to compare effect directionality must be done with caution.



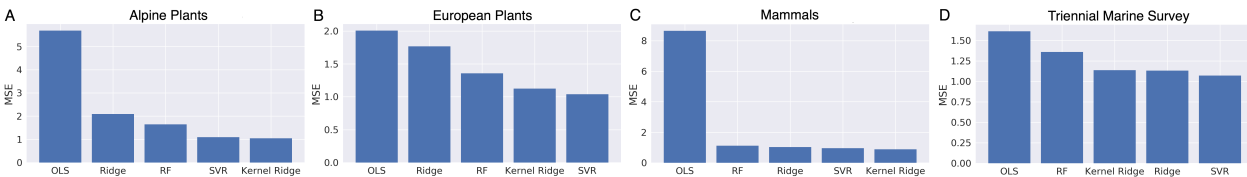
**Figure 3:** Models tend to agree on the variable importance values and directionality of top-ranking traits. We depict model coefficients (OLS, Ridge), Shapley feature importance values (Kernel Ridge, SVR), or Gini feature importance scores (RF) for top ten traits by rank (Figure 260 [ranks]) for each dataset (rows). Model abbreviations are as in Figure 1 and traits are as in Figure

2.

In summary, we find that non-linear methods increase predictive accuracy while identifying 265 similar predictive traits and directionality of the traits. Strong predictor traits are similar across the non-linear methods. These results are consistent across the four datasets examined in this study despite their taxonomic and geographic breadth.

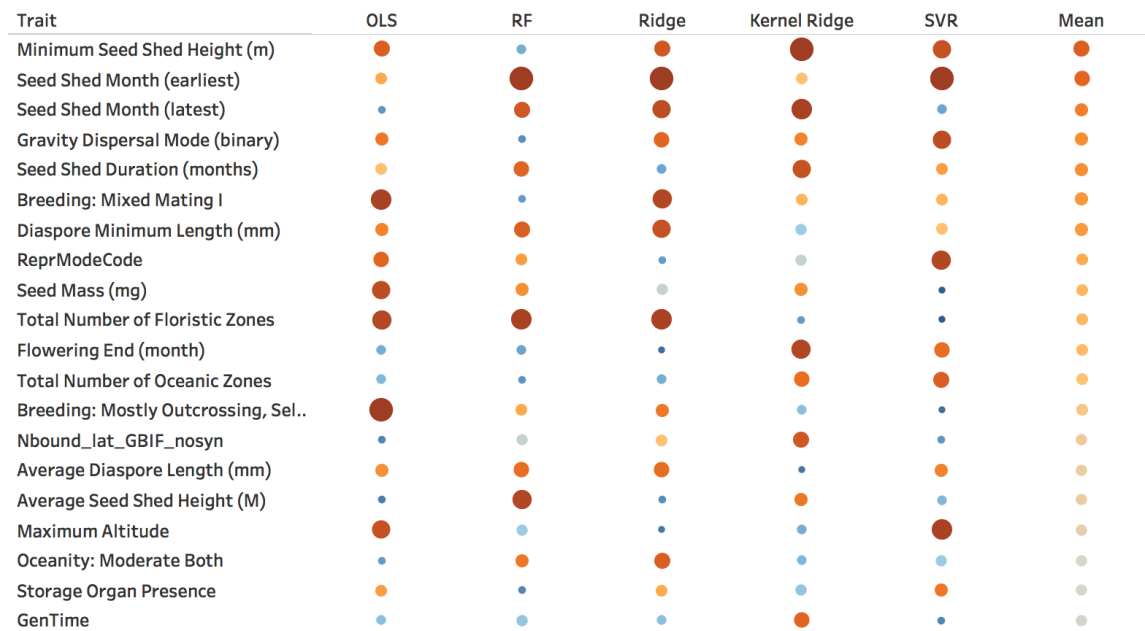
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**Figures and Figure Legends**

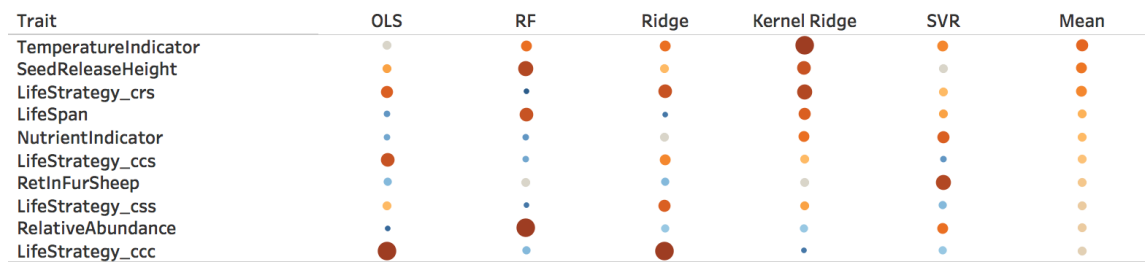


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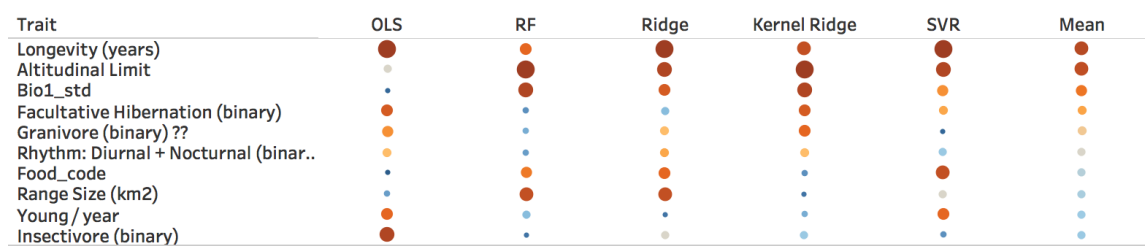
## A – Alpine Plants



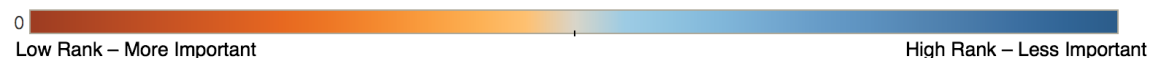
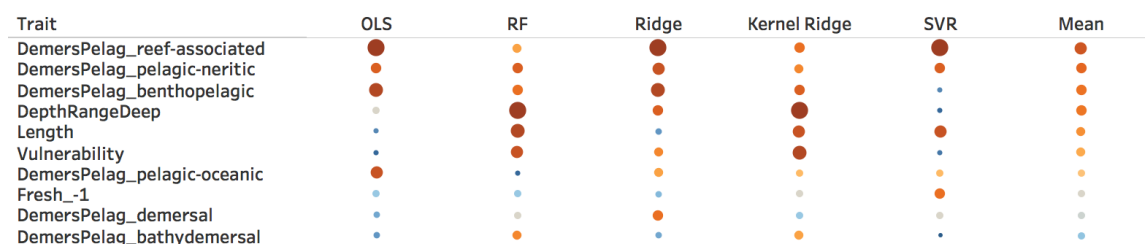
## B – European Plants



## C – Mammals



## D – Triennial Marine Survey

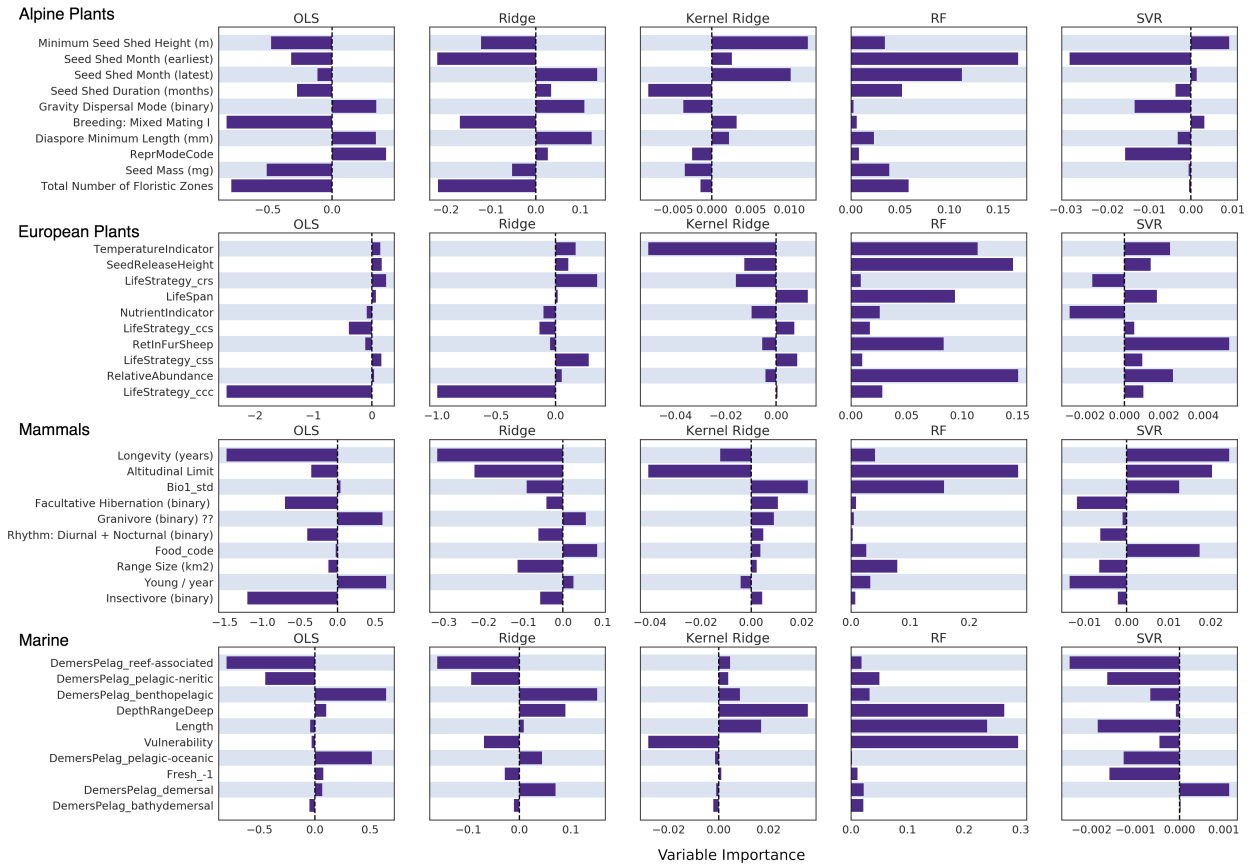




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## Discussion

295 Previous studies using linear modelling have found that species' traits are significant but weak predictors of variation in observed historical range shifts (Angert *et al.*, 2011; MacLean and Beissinger, 2017). We find that nonlinear modeling methods enhance the ability of traits to accurately predict observed range shifts. Our findings match biological intuition that biological processes, which respond to environmental conditions and are mediated by species' traits, are  
300 rarely linear (Stenseth and Mysterud, 2002). Importantly, we have also shown that the novel statistical models maintain biological rigor by identifying similar predictor traits. Models rank traits similarly despite methodological differences. This increases our confidence that these predictive models can be reliably employed in practical contexts to enhance decision-making in the face of climate change. In particular, extending species vulnerability frameworks to account  
305 for the non-linear influence of traits may enhance predictive ability and practical relevance.

Analysis frameworks such as ours that allow for non-linearities should be employed to further reevaluate expectations for how traits govern range shifts. Consideration of the processes associated with range shifts can help select predictor traits: four sequential processes underlying  
310 range shifts have been classified as emigration, movement, establishment, and proliferation [Estrada et al. 2016]. Generally, larger range shifts are expected for species with greater dispersal ability, reproductive potential, and ecological generalization [Buckley and Kingsolver 2012, MacLean and Beissinger 2017]. However, a meta-analysis across range shift studies found at best moderate support for dispersal ability (body size: 22%, migratory strategy: 10%, movement  
315 ability: 50%), reproductive potential (fecundity: 36%, longevity: 60%) and ecological generalization (diet breadth: 27%, habitat breadth: 43%) as predictors of range shift magnitude

(MacLean and Beissinger 2017). The large gap between expectations and observations highlights the need for novel predictive methods. Alternative expectations for traits such as ecological generalization further reinforces the need to allow for non-linear relationships between traits and climate change responses [Buckley and Kingsolver 2012]. Translating spatial range shifts into metrics of the extent to which species track their environmental niche (e.g., velocity of climate change, Loarie et al. 2009) may also enhance predictive capacity.

Our methodology—flexible statistical models paired with robust evaluation methods and model interrogation approaches—has been reliably employed across many predictive contexts (cite?), but has yet to be fully embraced by ecologists. The emerging wealth of publicly-available ecological and environmental data, combined with the pressing need for reliable ecological forecasts that are useful in decision-making frameworks, makes this flexible and data-intensive approach a natural fit. Despite promising results, our approach presents several challenges to adoption. Of particular relevance to the ecology community is the lack of traditional statistical techniques to evaluate these methods. Following the machine learning community, we employ  $k$ -fold cross-validation to lend statistical robustness to the pertinent evaluative criteria for our models (here, mean squared error). In addition, the use of recent advances in model inspection methods (Shapley values from Lundberg et al., 2017) represents a necessary departure from the manual inspection and testing of linear model coefficients. As the field of model interpretation grows, ecologists can leverage these developments to verify the ecological processes underpinning the predictions of these unconventional modeling approaches. Understanding and acknowledging these shifts in method evaluation and inspection approaches are critical steps to leveraging these more performant statistical modeling approaches in the ecology community.

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The general applicability of this approach should be confirmed by studies including additional taxa, a greater number of species, and using novel model interrogation techniques. In addition, the approach has the potential to improve predictive accuracy in other ecological domains relevant to policy and decisions making (species distribution modeling, forecasting of ecological carbon flux, etc.).

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### Acknowledgements

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