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Recommended Citation

Pardini, Eleanor A.; Drake, John M.; and Knight, Tiffany M., "On the utility of population models for invasive plant management: response to Evans and Davis" (2011). *Biology Faculty Publications & Presentations*. 18.

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Ecological Applications, 21(2), 2011, pp. 614–618
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On the utility of population models for invasive plant management: response to Evans and Davis

12 May 2010

To the Editor:

Recently we published an analysis of a model for the population dynamics of the invasive, biennial plant, *Alliaria petiolata* (Pardini et al. 2009). *Alliaria petiolata* is native to Eurasia and is a problematic invader of forest understories in the United States (Nuzzo 2000). In our paper, we parameterized a population model with field-collected data from one population at the Tyson Research Center (near St. Louis, Missouri, USA). We found that strong density dependence of *A. petiolata* at multiple stages in the life cycle should result in complex population dynamics (population cycles) and increased population density under some management scenarios. This result and other analyses of our model led us to two main conclusions that are relevant to management. First, we found that less than completely efficient management would have limited ability to curb *A. petiolata* densities to levels that would be considered desirable to land managers. Specifically, high adult mortality was required to reduce population densities and a wide range of intermediate levels of rosette management could even be counterproductive. Second, we concluded that managers should focus removal efforts on adult rather than rosette plants. Evans and Davis (2010) point out several errors in our model, as well as critique more subjective aspects of our model construction and our final management recommendations. We appreciate Evans's and Davis's careful and thorough attention to our paper. Here, we briefly note corrections to our model and we further respond to the other critiques of our model by Evans and Davis. We explain why we retain the fundamentals of our model interpretation and corresponding recommendations, with which they disagree. We also provide our computer code as a supplement to this reply, and our raw data upon request, so that others have complete access to our methods.

In this response, we (1) outline corrections to our statistical analyses and population model, (2) discuss the utility of population models such as ours for invasive species management, and (3) reevaluate management recommendations for *A. petiolata* based on the revised model. While the quantitative results of our model have changed, the qualitative results, and the management recommendations we draw from them, have not. In

contrast to Evans and Davis (2010), and in agreement with our earlier interpretation (Pardini et al. 2009), we continue to believe that the most sensible approach to management is to target an area that can be managed every year with high efficiency, and to focus efforts on plants in the adult stage class, for which high efficiency is possible. The utility of models in making management decisions, in our view, is to show the range and probability of behaviors that are possible, and to guide decisions that necessarily must be enacted given limited information. To do these things well, a model must be robust to minor structural and parameter estimation errors which are ubiquitous in models of nonlinear systems. Our analyses show that this robustness is a property of our modeling framework. To clarify our position, in what follows we propose and discuss criteria for the use of models in management of invasive species, focusing especially on qualitative vs. quantitative applications of model projections.

Statistical analysis and population model

Evans and Davis (2010) raise three main concerns with the model in Pardini et al. (2009): (1) statistical errors in analysis of rosette survivorship, (2) implementation of density-dependent rosette survival, and (3) modeling management interventions. In light of their critiques we have revisited our model and make three corrections which are outlined below.

1. *Statistical errors in analysis of rosette survivorship.*—In Pardini et al. (2009), summer survivorship, s_2 , was considered to be a function of rosette density (R), adult density (A), an interaction between the two ($U = A \times R$), and/or total density ($T = A + R$). Evans and Davis (2010) raise several concerns regarding the function for s_2 : a coding mistake and eventual typographical error resulting in a missing negative sign in the exponentiated term in the back transformation of the logistic regression formula are clear instances of error. While we respect the concerns that Evans and Davis (2010) raise about multicollinearity between U and T and the use of a model with an interaction term (U) but lacking main effects (R , A), we believe these concerns result from reasonable differences of opinion about statistical modeling strategy. Particularly, their concerns about multicollinearity are unwarranted and their Appendix B provided an extreme case in order to illustrate the potential effects of multicollinearity (whereas our regression had a variance inflation factor of 1.33, their example has a variance inflation factor of 12.16). Given the real mistakes in our analysis as well as concerns with multicollinearity and main effects, we re-ran the analysis and, using AIC selection, identified the following equation for summer rosette survivorship to August, given densities of rosettes (R_t) and adults (A_t) in May, which obviates concerns about collinearity and

lack of main effects:

$$s_2 = 1 / (1 + e^{-[0.11635 - 0.01612A_t - 0.00144R_t - 0.00092A_t R_t]}). \quad (1)$$

Evans and Davis (2010) raise additional concerns about our estimation of winter survivorship, s_3 , specifically the lack of an estimated intercept term and the transformation of the survivorship response variable. We reanalyzed the survivorship data using a logistic regression of survivorship of rosettes over winter, given rosette density in August (R_{Aug})

$$S_3 = 1 / \left(1 + e^{-[1.32702 - 0.50269 \ln(R_{\text{Aug}} + 1)]} \right). \quad (2)$$

The regression model for fecundity we selected and used in our population model, as originally published and now, is

$$f = e^{7.48933 - 0.03893A_t}. \quad (3)$$

The raw data and fitted functions described above are depicted in Appendix A. Results of the population model with revised equations for density-dependent rosette survivorship are shown in panels D and E of Appendix B.

2. *Implementation of density dependence.*—Evans and Davis (2010) raise a concern about the representation of seasonal density-dependence in our model, specifically rosette survivorship over the winter. The population model in Pardini et al. (2009) was parameterized such that s_3 was a function of R_t , where t implicitly refers to May in a May-to-May transition model [i.e., $A_{t+1} = R_t s_2(R_t, A_t) s_3(R_t)$]. The model coefficients we used, however, were estimated from data collected in August. Effectively, our parameterization treated May rosette density as an estimator of August rosette density. Evans and Davis (2010) propose an alternative model where winter survivorship is a function of rosette densities in August (R_{Aug} ; i.e., $A_{t+1} = R_t s_2[R_t, A_t] s_3[R_{\text{Aug}}] = R_t s_2[R_t, A_t] s_3[R_t s_2(R_t, A_t)]$). The results of our model using the original (panels D and E) and the realistic (panels G and H) implementations of density-dependent winter rosette survivorship are depicted in Appendix B. A comparison of the two implementations shows that the branching structure of the bifurcation diagram is unchanged but that the locations of the bifurcation with respect to the x -axis (induced mortality through culling) and the maximum population size are shifted.

3. *Modeling management.*—Representing management actions in a stage-structured model, especially one that includes density-dependent vital rates, is complex. Particularly, the timing of actions relative to the census point and which vital rates are affected must be considered carefully because, even though natural systems may respond immediately, model trajectories are not continuously updated. In Pardini et al. (2009), we stated that “we simulated induced mortality of adults (e.g., applying herbicide or hand-pulling adults in the

spring) or of rosettes (e.g., applying herbicide in the fall).” Our model code, however, was designed explicitly to investigate the effects of managing rosettes and adults in the spring, immediately prior to the census point (May). When rosette management is applied at this point, density-dependent summer and winter survivorship both proceed without changes to the rosette numbers entering these intervals, but the number of rosettes that proceed to the adult stage is reduced by a one-time mortality event (M_R). To represent adult management, we reduced the number of adults contributing seeds to the S and R stages by a mortality parameter M_A , but as Evans and Davis (2010) note, our model did not include the effect of removing adults in May on survivorship of neighboring rosettes. Since summer survival of rosettes is indeed higher when adults are removed (Winterer et al. 2005, Pardini et al. 2008), this is a necessary adjustment. A revised set of equations given rosette (M_R) and adult management (M_A) is

$$S_{t+1} = v(1 - g_1)(1 - M_A)A_t f(A_t) + (1 - g_2)S_t \quad (4a)$$

$$R_{t+1} = v g_1 s_1 (1 - M_A) A_t f(A_t) + g_2 s_1 S_t \quad (4b)$$

$$A_{t+1} = (1 - M_R) R_t s_2 \left(R_t, (1 - M_A) A_t \right) \times s_3 \left[R_t s_2 \left(R_t, (1 - M_A) A_t \right) \right]. \quad (4c)$$

This set of equations is equivalent to Eqs. A5a–d presented in Appendix A of Evans and Davis (2010) and corresponds to the model code provided as an online supplement to this paper. These adjustments to adult management result in quantitative, but not qualitative, changes to the bifurcation structure of the model (compare panels B, E, and H [original procedure] with panels C, F, and I [corrected procedure] of Appendix B). Note that panels A and B of our Appendix B show results originally presented in Pardini et al. (2009) and correspond to Fig. A.1, panels a and b in Appendix B of Evans and Davis (2010), and our best understanding of this system at this time is shown in panels G and I, which correspond to Fig. A.1, panels i and j in Evans and Davis (2010).

In conclusion, the current working model of this system has been revised to include a more complicated model of density-dependent winter rosette survivorship and effects of adult management on all life stages. While the corrected model with the new adult management procedure (Appendix B, panel I) does not produce chaotic dynamics at intermediate levels of adult mortality (presumably a relatively fragile result in the model of Pardini et al. (2009) in any case), it does produce complex, cyclic dynamics and indicates that high adult mortality is required to reduce the population to single equilibrium conditions and low density. The impact of rosette management in the revised model (Appendix B,

panel G) is not as dramatic as in the model of Pardini et al. (2009), but the general patterns (cyclic population dynamics, maximum population densities at intermediate levels of management, and the requirement of high management efficiency to reach single equilibrium dynamics and desirable low densities) all remain. Further, we interpret these qualitative outcomes of our model to be robust to variation in early survival s_1 . If one is interested in reducing population density to levels below the original low density in a cycling population, the result remains across values of s_1 that most levels of induced mortality produce cyclic dynamics and mortality must be high to effectively curb population density. Accordingly, these modifications do not substantially change our main finding: density dependence at multiple life stages produces complex dynamics (population cycles) and incomplete control efforts have limited ability to curb population densities or may even backfire. Thus, it follows from our current understanding of this system that high removal efficiency should be an objective of any management strategy.

Utility of models for invasive species management

As noted above, Evans and Davis (2010) identified for us both errors in our original analysis and improvements that could be made to our model. In our view, some of the other points they raise (e.g., concerning suitability of hypothesis tests, inclusion of interactions, realism vs. parsimony in model formulation, and so on) reflect a difference in philosophies of scientific and statistical modeling; the range of reasonable and acceptable opinions on these issues is quite broad. In a famous quote, Box and Draper (1987) state that, "all models are wrong, but some are useful." Even very complex models are simplified representations of nature, and no model can be expected to capture all possible complexities of a population's dynamics. In our view, the trade-off between simplicity and complexity involves both strategic decisions (What is the purpose of the model?) and empirical criteria (What level of complexity is warranted given the data?). Since model purpose is an ineliminable and subjective component of the model building process, no purely formal approach to determining model complexity (e.g., AIC) is authoritative. These issues are accentuated in applied sciences (such as invasive species management) where societal aims, expectations, and standards of evidence are forefront.

There has been much discussion in the literature about what types of model conclusions are useful. An important distinction in the interpretation of mathematical models is that of forecasting versus projection: forecasts predict what *will* happen; projections predict what *would* happen given an assumed set of conditions (Keyfitz 1972). The utility of population projections is widely accepted because they reveal behavior under current conditions, not because they predict future

outcomes (Caswell 2001). Evans and Davis (2010) focus on issues of parameter estimation and inference space to a point that it overshadows the utility of this model as a projection tool. Ecologists tend to agree that many models are useful in their qualitative conclusions, such as identifying the scope of what is possible and comparing the relative benefits of alternative management options, to guide discussion and evaluation. Fewer models are useful in their precise quantitative predictions, e.g., forecasted population sizes, locations of bifurcations, and precise rates of minimal management efforts that will achieve target population densities. Particularly, recent reviews have concluded that structured models likely will not make precise forecasts of population numbers even when multiple populations and years are sampled and used in estimation, that research should focus on methods to reduce uncertainty, and that numerical confidence is typically misplaced (e.g., Caswell 1989, Bierzychudek 1999, Menges 2000, Coulson et al. 2001, Reed et al. 2002). It does not follow, however, that models are useless unless they are numerically accurate. At the very least, population models represent sophisticated thought experiments of the form "if nature works as X and we take action Y , then . . ." In this respect, population models are at least as reliable as expert opinion and are superior insofar as they expose counterintuitive phenomena in complex systems (e.g., nonlinear feedbacks that cause management actions to backfire).

Models may thus be extremely useful in research on the population dynamics of invasive species. In a recent review, Ramula et al. (2008) identified a total of 22 published studies that used matrix population models to examine population dynamics of invasive plant species. As with our study of *A. petiolata*, most of these involved only a single study site (15 out of 22). In nearly all studies, management applications that might be useful to practitioners studying the invasive species at other sites were discussed. Further, many of these studies (eight out of 15) were published in journals that have a mission to support environmental decision-making and to be accessible to both scholars and practitioners, such as *Ecological Applications* and *Journal of Applied Ecology*. Evans's and Davis's (2010) statement that our model's inference space cannot reach beyond our single study site is extreme. In our view, if one must act in the world and the data that are needed to act deliberately and confidently in a particular system are unavailable, then the next best thing is to turn to a similar system for lessons learned.

The reality of on-the-ground management necessitates that managers make informed decisions given the available information. Science-based management almost always involves extrapolations from studies conducted at particular times and places to other populations. Managers must collect available informa-

tion about their target species (e.g., life history, population biology, response to herbicides) from other sites and times, and even about other invasive species (i.e., How do biennial weed populations typically respond to herbicide?) and then decide, given what they know about the conditions under which the information was collected, how to use it. The narrow focus on parameter estimation and quantitative predictions of models that Evans and Davis suggest would debilitate management efforts. If the focus is instead on the qualitative insights provided by our study (Is management efficiency important? Can management actions backfire? Which stage class should be the focus of control efforts?), then our results provide a valuable contribution that should help managers think through their strategies for managing *A. petiolata* and other species at uncontrolled and unstudied locations.

Management implications for A. petiolata

In Pardini et al. (2009), we concluded that invasive species similar to *A. petiolata* (i.e., short-lived species with seed banks that experience strong density dependence) may display complex population dynamics and thus may be difficult to manage, requiring strategies that are highly efficient and applied every year. For *A. petiolata* we recommended that management should be highly efficient, applied annually, focused on adults, and targeted in space to achieve maximum efficiency. Evans and Davis (2010) deemed these recommendations inappropriate in their scope and expressed concern that they are currently being implemented by natural areas managers. We find that quantitative and structural corrections to our model presented here result in quantitative changes to the results but in our opinion do not alter the fundamentals of the qualitative results nor the corresponding recommendations we would draw from them. We hope that when planning how to allocate available resources, managers will continue to consider management efficiency, that backfiring is a possibility of certain actions, and that for species such as *A. petiolata*, focusing management on stage classes for which high removal efficiency can be achieved should be a top priority.

For this population of *A. petiolata*, we found with our original and corrected model that strong density dependence at multiple stages in the life cycle may result in complex, cyclic population dynamics. Species with complex dynamics should be difficult to manage because reductions in density through management are counteracted by increased fitness of surviving individuals released from density-dependent regulation (Myers et al. 1989, Buckley et al. 2001). Thus, for these types of populations, management will not be successful until high levels of management efficiency are achieved. For our model and study site, while the exact level of

mortality required to produce single equilibrium dynamics is lower with the revised model, the level required to curb the density below the low density of the cycling population in the absence management remains very high.

In our original paper, we emphasized both quantitative and qualitative results of our model. Here we wish to emphasize that it is the qualitative recommendations we drew that are most important, and these have not changed. The exact level of efficiency required depends on the management goal (e.g., to reduce the population to a low density versus to completely eradicate) and, of course, will differ among populations. Focusing on the exact levels of eradication required distracts from the more important point that management efficiency is an important issue to consider. These considerations lead us to make several qualitative recommendations. First, it is important to think about efficiency when deciding how to distribute available resources and effort. When employing volunteers to manage invasive plants such as *A. petiolata*, managers should prioritize important target areas and prevent volunteers from spreading out in space until every plant in the focal area is killed. Otherwise, volunteers might move on to areas that are easy to manage (e.g., areas with higher adult density), rather than spending extra time finding the last few plants in the target area. Second, managers should target adult plants rather than rosettes, given the management tools that are currently typically employed. Adult plants are often managed by hand pulling, a strategy through which high efficiency can be achieved. First-year rosette plants are often managed with herbicide in the fall or early spring when other native plants are present in low densities. However, it is difficult to achieve high removal efficiency with herbicide because seedlings may be hidden under leaf litter, and some seedlings might germinate after the management has been implemented. Another option that may become widely considered for targeting rosette plants is biocontrol, but efficiency will need to be considered when evaluating potential for success (e.g., Gerber et al. [2007] reported a 43% reduction in rosette survival by *Ceutorhynchus scrobicollis* in field tests). Given that density dependence in the seedling stage is high and only a fraction of individuals survive to become fruiting adults, it might be better to instead target resource efforts on managing easily visible adults.

Acknowledgments

We thank Jeffrey Evans and Adam Davis for engaging in a critical discussion of these models. We also thank Hal Caswell, Elizabeth Crone, Ruth Hufbauer, and Drew Kramer for comments that improved the manuscript and Nick Griffin for assistance with figures. The original research was supported by funding from the USDA CSREES, #05-2290, the University of Georgia Odum School of Ecology, and Washington University's Tyson Research Center.

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APPENDIX A

Raw data and revised density-dependent functions for rosette survivorship and adult fertility (*Ecological Archives* A021-033-A1).

APPENDIX B

Corrections to garlic mustard SRA model (*Ecological Archives* A021-033-A2).

SUPPLEMENT

R code for the SRA population model for *Alliaria petiolata* described in this paper (*Ecological Archives* A021-033-S1).