



Predicting Recovery Criteria for Threatened and Endangered Plant Species on the Basis of Past Abundances and Biological Traits

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Abstract: Recovery plans for species listed under the U.S. Endangered Species Act are required to specify measurable criteria that can be used to determine when the species can be delisted. For the 642 listed endangered and threatened plant species that have recovery plans, we applied recursive partitioning methods to test whether the number of individuals or populations required for delisting can be predicted on the basis of distributional and biological traits, previous abundance at multiple time steps, or a combination of traits and previous abundances. We also tested listing status (threatened or endangered) and the year the recovery plan was written as predictors of recovery criteria. We analyzed separately recovery criteria that were stated as number of populations and as number of individuals (population-based and individual-based criteria, respectively). Previous abundances alone were relatively good predictors of population-based recovery criteria. Fewer populations, but a greater proportion of historically known populations, were required to delist species that had few populations at listing compared with species that had more populations at listing. Previous abundances were also good predictors of individual-based delisting criteria when models included both abundances and traits. The physiographic division in which the species occur was also a good predictor of individual-based criteria. Our results suggest managers are relying on previous abundances and patterns of decline as guidelines for setting recovery criteria. This may be justifiable in that previous abundances inform managers of the effects of both intrinsic traits and extrinsic threats that interact and determine extinction risk.

Keywords: delisting criteria, Endangered Species Act, extinction risk, recovery, species tree-based statistical models

Predicción de Criterios de Recuperación para Especies de Plantas en Peligro y Amenazadas con Base en Abundancias Pasadas y Atributos Biológicos

Resumen: Los planes de recuperación para especies enlistadas en el Acta de Especies en Peligro de E.U.A. deben especificar criterios medibles que pueden ser utilizados para determinar cuando se puede suprimir de la lista a la especie. Para las 642 especies de plantas enlistadas en peligro o amenazadas y que tienen planes de recuperación, aplicamos métodos de partición recursiva para probar si se podía predecir el número de individuos o poblaciones que se requieren para suprimir de la lista a la especie con base en atributos de la distribución y biológicos, en la abundancia previa en múltiples frecuencias temporales, o en una combinación de atributos y abundancias previas. También probamos como predictores de criterios de recuperación al estatus en la lista (amenazada o en peligro) y el año en que se escribió el plan de recuperación. Analizamos por separado los criterios de recuperación definidos como número de poblaciones y como número de individuos (criterios basados en poblaciones y basados en individuos, respectivamente). Las abundancias previas por sí solas fueron predictores relativamente buenos de criterios de recuperación basados en poblaciones. Se requirieron menos poblaciones, pero una mayor proporción de poblaciones conocidas históricamente, para suprimir de la lista a especies que tenían pocas poblaciones cuando fueron enlistadas en comparación con

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especies que tenían más poblaciones al ser enlistadas. Las abundancias previas también fueron buenos predictores de criterios basados en individuos cuando los modelos incluyeron tanto abundancias como atributos. La división fisiográfica en la que ocurren las especies también fue un buen predictor de criterios basados en individuos. Nuestros resultados sugieren que los manejadores están confiando en abundancias previas y patrones de declinación como lineamientos para definir criterios de recuperación. Esto puede ser justificable debido a las abundancias previas informan a los manejadores sobre los efectos tanto de atributos intrínsecos como de las amenazas extrínsecas que interactúan para determinar el riesgo de extinción.

Palabras Clave: Acta de Especies en Peligro, criterios para suprimir de la lista, modelos estadísticos basados en árboles, recuperación de especies, riesgo de extinción

Introduction

The primary goal of the U.S. Endangered Species Act (ESA) is to recover species such that they are no longer in danger of extinction (endangered) or at risk of becoming endangered in the foreseeable future (threatened). Measurable criteria (e.g., threshold numbers of populations or individuals that would indicate species recovery and allow delisting) have been required since passage of a 1988 amendment to the ESA (section 4[f]1). This is generally considered a positive requirement because species with measurable criteria are more likely to show improved status than species without such criteria (Gerber & Hatch 2002). However, existing criteria have been criticized for being too low (Tear et al. 1995; Neel et al. 2012), for not being based on biological characteristics (Elphick et al. 2001), and for being based on guesswork (Schemske et al. 1994).

Although the criteria are easy to criticize, there is little scientific guidance regarding exactly how many individuals or populations are necessary and sufficient for species persistence (Sanderson 2006). There is, however, extensive empirical evidence and theory relating general probability of extinction to abundance. More and larger populations over broader geographic areas are more likely to persist because, all else being equal, extinction risk is higher for small versus large populations (Gabriel & Burger 1992; Blackburn & Gaston 2002; Matthies et al. 2004), for species with small versus large ranges (Gaston 1994), for habitat specialists (Farnsworth & Ogurcak 2008), and for species with a small or declining number of populations (Hanski et al. 1995) or range size (Channell & Lomolino 2000). The challenge lies in translating these general associations into quantitative criteria that reduce extinction risk such that species are no longer in danger of extinction throughout all or a significant portion of their range and are not likely to become so in the foreseeable future (ESA sec. 3[20]). Although results of previous research indicate more is better, there is no theoretical basis for saying, for example, that conserving 8 populations does not sufficiently reduce extinction risk to a level that warrants delisting, whereas conserving 9 populations is sufficient and conserving over 10 populations is more than sufficient. Furthermore, relations between

abundance and extinction risk are highly dependent on extrinsic threats (Neel et al. 2012).

Still, it is considered desirable that criteria for listed species be consistent or predictable, following assumptions that species sharing biological characteristics have similar extinction risks in comparable situations and should respond similarly to management interventions. However, past evaluations show that recovery criteria vary tremendously (Tear et al. 1993; Neel et al. 2012) and are not consistently related to biological traits. For example, numbers of individuals required to delist 27 bird species were best predicted by numbers of individuals existing at the time the recovery plan was written, not by body mass, fecundity, or lifespan (Elphick et al. 2001). Similarly, numbers of populations required to delist 98 plant species were correlated with numbers of populations at plan writing (Schemske et al. 1994).

We used tree-based statistical models to determine whether recovery criteria for 642 plant species listed under the ESA for which recovery plans were approved as of January 2010 are based on distribution and biological traits, previous abundances, or a combination of traits and previous abundances. Tree-based methods are increasingly used to examine extinction risk (Davidson et al. 2009; Bielby et al. 2010; Murray et al. 2011) because they excel at identifying contingent associations and make no assumptions about underlying variable distributions. We expanded on Schemske et al.'s (1994) work to provide further insight into the determinants of recovery criteria by examining many more species, incorporating abundances at multiple time steps, and considering measures of recovery for both populations and individuals.

Methods

Variables

We quantified 3 sets of variables in recovery plans: delisting criteria (responses), previous abundances (predictors), and distribution and biological traits (predictors). Of the 642 species we examined, 438 had quantitative delisting criteria stated as number of populations (population-based criteria; $n = 427$) or individuals (individual-based criteria; $n = 314$ for number of

individuals per population $n = 324$ for total number of individuals). The remaining 204 species were considered by plan authors as too imperiled or data deficient to be delisted, and efforts to recover these species focused on preventing extinction. We considered previous abundances as the number of populations known historically, at time of ESA listing, when the plan was written, and as the total number of individuals at listing and when the plan was written (Table 1). The historical period was the time before anthropogenic decline, but it was necessarily vague because dates were not typically given in plans. We considered delisting criteria as number of individuals per population, total number of individuals, number of populations, and proportion of the historical number of populations represented by the number of populations required for delisting (Table 1). Lack of data on individual-based historical abundances precluded calculating the proportion of historical number of individuals represented by the delisting criteria.

We analyzed 8 distribution and biological traits (hereafter traits) (Table 2), which represented a compromise between variables that relate to extinction risk and rarity and those for which estimates were available for a sufficient number of species to allow analyses. As a measure of geographic location, we included physiographic division (Fenneman & Johnson 1946) (Appalachian Highlands, Arctic, Atlantic Plain, Canadian Shield, Hawaii and Pacific Islands, Interior Highlands, Interior Plains, Intermontane Plateaus, Pacific Mountain System, Rocky Mountain System, West Indian) in which each species occurs. We initially included year of recovery-plan approval and listing status when the plan was written (threatened or endangered) as predictor variables because they were examined in an earlier study of recovery criteria (Elphick et al. 2001). However, they had low variable-importance values and are not strictly biological traits; thus, we excluded them from final analyses. We also excluded taxonomic family because it contained too many levels (109 families) to be included in random forest (RF) analyses and was not a consistent splitting variable in conditional inference trees.

Analyses

We used RFs to analyze relations between predictors and delisting criteria. RF is an ensemble classification- and regression-tree method in which data are partitioned recursively into groups of increasingly similar observations on the basis of predictor variables (Breiman et al. 1984). Ensemble-tree methods provide more robust predictions than single trees because they average results over a set of trees built from bootstrap samples of observations (Breiman 2001; Strobl et al. 2009). We implemented RF with the randomForest function in the R package randomForest (Liaw & Wiener 2002). We calculated importance of predictor variables as the mean increase in prediction

Table 1. Summary of quantitative delisting criteria and abundance estimates for all plant species listed as threatened or endangered under the U.S. Endangered Species Act.

	Including Hawaiian species					Excluding Hawaiian species				
	<i>n</i>	<i>minimum</i>	<i>median</i>	<i>maximum</i>	<i>mean (SD)</i>	<i>n</i>	<i>minimum</i>	<i>median</i>	<i>maximum</i>	<i>mean (SD)</i>
Number of populations										
historical	410	1	8	475	17 (350)	219	1	8	475	23 (47)
at listing	418	0	3	173	7 (14)	240	1	3	173	9 (17)
when plan was written	604	0	5	231	11 (22)	359	0	6	231	15 (27)
required for delisting	427	1	8	117	11 (11)	181	1	12	117	16 (16)
proportion of historical	296	0.04	1	8	1.54 (1.67)	105	0.04	0.88	6	1.17 (1.13)
required for delisting										
Number of individuals										
at listing	381	0	125	1,500,000	7898 (79,806)	168	1	520	1,500,000	17,492 (119,691)
when plan was written	479	0	275	1,000,043,766	239,731 (4,574,310)	236	0	2,000	100,043,766	486,006 (6,514,667)
required for delisting	324	400	2400	1,300,000	10,739 (74,178)	78	400	12,000	1,300,000	38,087 (148,601)
number per population	314	5	300	50,000	745 (3417)	68	5	500	50,000	2,504 (7,108)
required for delisting										

error when values for that variable were randomly permuted. We used functions *cforest* and *varimp* (specifying *conditional = true*) in the R package *party* to run conditional random forests (cRF). When calculating variable importance, cRF adjusts for correlations between predictors and produces unbiased variable selection (Hothorn et al. 2006; Strobl et al. 2008). For both ensemble-tree methods, we built 1000 trees, with 4 randomly chosen predictors tested at each node (*mtry* = 4) and default values for all other parameters. Different *mtry* values were tested and produced similar results. When there were fewer than 4 predictors in the model, *mtry* equaled the total number of predictors (method called bagging). We constructed partial-dependence plots (predicted regression function between predictor and response) to examine marginal effects of predictors with highly variable importance values.

To visualize predictor effects and validate results from RF and cRF, we generated conditional inference trees (cTree) with the *cTree* function in the R package *party*. Although single-tree methods are more sensitive to small changes in the data than ensemble methods, they produce easily interpretable diagrams depicting partitioning of species by predictors. We set the *p* value for rejecting the null hypothesis of no association between the response and any predictor at 0.05 and used default values for other parameters.

We assessed model accuracy by quantifying model prediction error. For cTree we used the mean squared error between actual delisting criteria and those predicted by the model. For RF and cRF, we used the out-of-bag prediction error (mean squared error calculated from observations not used to build individual trees). To allow comparison, we standardized error rates as the percentage of variance explained, or $[1 - (\text{error}/\text{variance in the response})] \times 100$ (Liaw & Wiener 2002). Negative values result when prediction errors are greater than variance in the data and indicate poor model accuracy.

We used traits alone, previous abundance alone, and both abundance and traits in 3 sets of analyses to predict delisting criteria (i.e., number of individuals or populations required to delist). Within each set, we ran separate analyses for each delisting criterion (Table 3). We also ran analyses with and without Hawaiian species ($n = 245$), which had nearly identical delisting criteria (8 populations and 80, 100, or 300 individuals per population) and thus could strongly affect the results. When the delisting criterion was proportion of historical populations, we did not exclude Hawaiian species because although their absolute criteria were the same, the historical number of populations varied substantially and thus the proportions also varied. Because missing values precluded calculating variable importance in cRF, we used different subsets of species ($n = 18\text{--}257$) in different analyses. Specifically, abundance-only models were built with a larger data set than models including abundance and traits

Table 2. Distribution and biological traits included in our analyses as predictors of quantitative delisting criteria for all plant species listed under the U.S. Endangered Species Act.

<i>Trait</i>	<i>Levels within each trait^a</i>
Maximum plant height (m)	continuous (491/337)
Maximum flower size (cm)	continuous (325/200)
Life form	herb (333/282), lichen/moss (3/2), shrub (133/48), subshrub (44/18), tree (106/40), or vine (23/7)
Life history duration	annual (79/75), perennial (380/302), or short-lived perennial (192/28); some species fell in more than one category (9/8)
Reproductive mode	clonal (3/3), clonal and sexual (132/107), or sexual (504/285)
Reproductive repetition	monocarpic (85/82) or polycarpic (553/312)
Physiographic division (after Fenneman & Johnson 1946) ^b	Appalachian Highlands (49/49), Arctic (1/1), Atlantic Plain (82/82), Canadian Shield (2/2), Hawaii and Pacific Islands (320/25), Interior Highlands (6/6), Interior Plains (36/36), Intermontane Plateaus (64/64), Pacific Mountain System (113/110), Rocky Mountain System (7/7), West Indian (50/50); some species fell in more than one category (25/25), creating 23 distinct combinations of divisions
Range area (m ²) ^c	continuous (483/292)
Listing status ^d	endangered (536/298), threatened (106/99)

^aNumber of species for which there are data is in parentheses (number including Hawaiian species/number excluding Hawaiian species).

^bWhen physiographic division was not stated directly we determined it by comparing species distributions listed in recovery plans with a digital coverage of divisions (Fenneman & Johnson 1946).

^cEstimated as the intersecting area between the physiographic section and the state distribution listed in the recovery plans.

^dAlthough not included in final analyses, listing status at the time the plan was written is included to show number of species in each category in our data set.

because data for both abundance and traits were available for fewer species. To fairly compare the models, we also ran abundance-only or traits-only models (whichever provided a better fit for each delisting criterion) with the reduced data set of species that was used in analyses including all trait and abundance variables. In total, there were 28 models from combinations of the 4 delisting criteria, 3 sets of predictors, whether Hawaiian species were included, and whether the largest possible data set or the reduced data set was used (Table 3).

Results

Previous Abundances as Predictors

Previous abundances alone explained 37–71% of variance in number of populations required for delisting for all

Table 3. Summary of analyses of the quantitative delisting criteria for all plant species listed under the U.S. Endangered Species Act organized by delisting criterion (number of populations, proportion of historical populations, number of total individuals, and number of individuals per population required to delist a species) and type of predictor variable (traits only, abundance only, or abundance and traits).^a

Variable ^b	Number of populations				Proportion of historical populations			
	traits only	abundance only	abundance and traits	abundance only - reduced ^c	traits only	abundance only	abundance and traits	abundance only - reduced ^c
<i>n</i> (with HI species) ^d	139	205	66	66	92	205	66	66
<i>n</i> (without HI species)	55	69	19	19	NA	NA	NA	NA
Population abundance								
no. pop. historical		x	x	x		x*	x	x
no. pop. listing		x*	x*	x		x	x	x
no. pop. writing		x	x*	x		x	x	x
no. pop. listing/historical						x*	x	x
no. pop. writing/historical						x	x	x
Trait								
maximum height	x		x		x		x	
maximum flower size	x		x		x		x	
life form	x		x		x		x	
life-history duration	x		x		x		x	
reproductive mode	x		x*		x		x	
reproductive repetition	x		x*		x		x	
physiographic division	x		x		x		x	
range size	x		x		x		x	
Variance explained (%) ^e								
cTree	20.67	59.71**	34.69**	19.29	-0.0043	67.95**	32.31	61.56
RF	-22.33	70.90**	48.76**	10.38	-12.66	63.97**	65.19	52.09
cRF	4.20	36.92**	13.22**	12.68	-2.90	63.19**	33.42	35.74
cTree (no HI)	-0.0019	62.37**	-0.0020	0.0061				
RF (no HI)	-37.44	78.70**	39.77	30.61				
cRF (no HI)	-9.48	36.88**	-11.19	-11.35				
Variable ^b	Number of total individuals				Number of individuals per population			
	traits only	abundance only	abundance and traits	traits only - reduced ^c	traits only	abundance only	abundance and traits	traits only - reduced ^c
<i>n</i> (with HI species) ^d	114	257	91	91	110	253	90	90
<i>n</i> (without HI species)	31	45	19	19	27	41	18	18
Individual abundance								
no. indiv. listing		x	x*			x	x*	
no. indiv. writing		x	x*			x	x*	
Trait								
maximum height	x		x	x	x		x	x
maximum flower size	x		x	x	x		x	x
life form	x*		x*	x*	x		x	x
life-history duration	x*		x*	x	x		x*	x
reproductive mode	x		x	x	x		x	x
reproductive repetition	x		x	x	x		x	x
physiographic division	x*		x*	x*	x		x*	x
range size	x		x	x	x		x	x
Variance explained (%) ^e								
cTree	57.84**	-0.0028	53.92**	55.64**	44.97	0.0003	47.54**	47.54
RF	44.51**	-55.52	56.12**	35.05**	4.63	22.28	19.7**	10.38
cRF	46.32**	-2.84	31.43**	40.85**	20.41	10.96	22.07**	16.94
cTree (no HI)	-0.0023	-0.0009	-0.0022	-0.0049	22.90	0.0017	0.0011	0.0008
RF (no HI)	10.67	-63.12	30.32	-0.14	-5.85	13.2	-2.07	-9.42
cRF (no HI)	-1.63	-8.17	-11.76	-12.12	-7.70	5.79	-12.49	-13.06

continued

Table 3. continued

^aAn *x* indicates the variable was included in an analysis and an asterisk (*) indicates the variable was identified as an important predictor variable by any of the 3 modeling methods used.

^bKey: no. pop. historical, number of historically known populations; no. pop. listing, number of populations at time of listing; no. pop. writing, number of populations when plan was written; no. pop. listing/historical, proportion of historical populations remaining at time of listing; no. pop. writing/historical, proportion of historical populations remaining at time of plan writing; no. individ. listing, number of individuals at time of listing; no. indiv. writing, number of individuals at time of plan writing; life-history duration, whether species was annual, perennial, or short-lived perennial; reproductive repetition, whether species was monocarpic or polycarpic; physiographic division, measure of geographic location in which the species occurs.

^cModels built with data from only the species with no missing values in any of the abundance and trait variables.

^dSample sizes (*n*) varied when Hawaiian (HI) species were excluded and when different predictors were used due to missing values.

^ePrediction error standardized by variance for each analysis by modeling method (cTree, conditional inference tree; RF, random forest; cRF, conditional random forest; random forest is an ensemble classification- and regression-tree method in which data are partitioned recursively into groups of increasingly similar observations on the basis of predictor variables) and for models excluding Hawaiian species (no HI) (**, models with the highest percent variance explained).

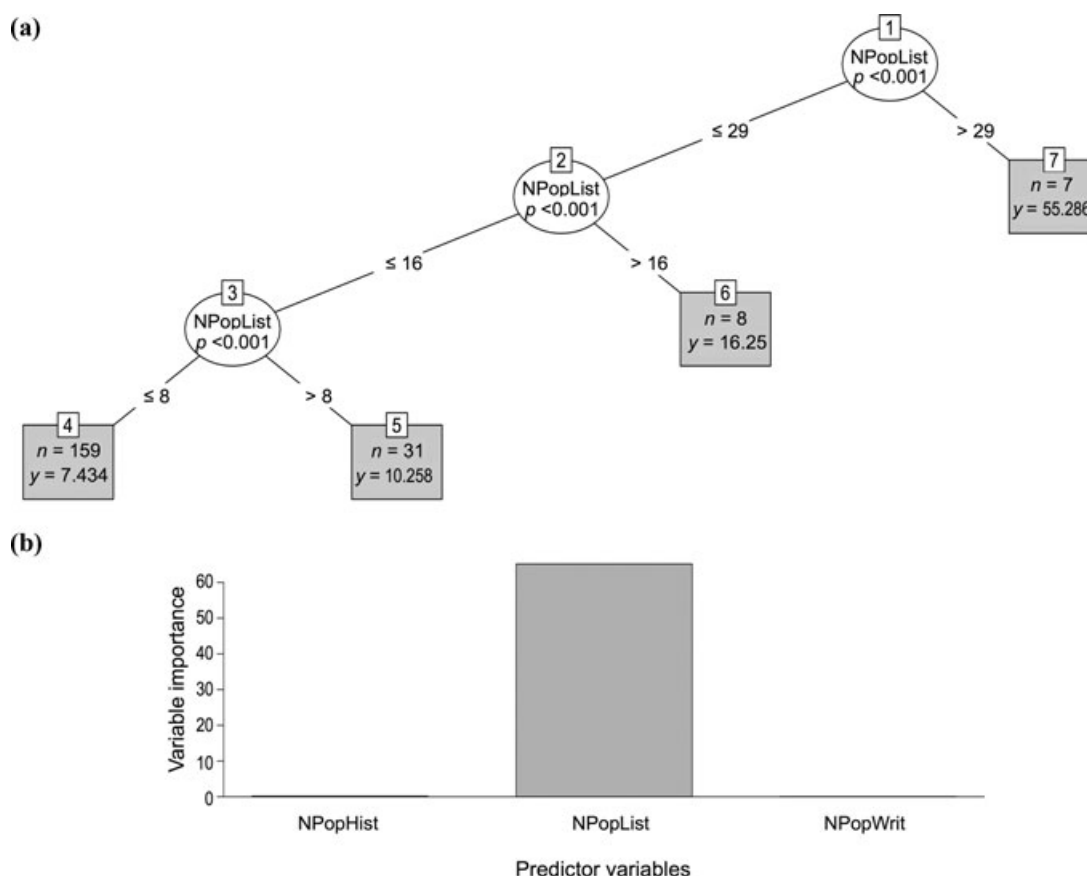


Figure 1. Results of analysis of the number of populations required for delisting under the U.S. Endangered Species Act on the basis of previous abundance (NPopHist, number of historical populations; NPopList, number of populations at time of ESA listing; NPopWrit, number of populations when recovery plan was written) as predictor variables and including Hawaiian species ($n = 205$): (a) conditional inference tree diagram (shows how important predictor variables divide species into groups with similar response values) and (b) variable importance values from conditional random forest analysis, measured as the mean increase in model error (units are number of populations) when each predictor variable is randomly permuted.

species and 37–79% of variance when Hawaiian species were excluded (Table 3). The cTree and cRF identified only number of populations at listing as an important predictor variable. For example, cTree indicated on average 55.3 populations were required to delist species with

>29 populations at listing, and 16.3 populations were required to delist species with 17–29 populations at listing (Fig. 1a). In cRF model-prediction error increased by 60 units (populations) when the number of populations at listing was randomly permuted (Fig. 1b). In contrast,

RF assigned high importance values to both number of populations at listing and when the plan was written. The difference between modeling methods suggested high correlation between abundances at listing and when the plan was written because RF assigns high importance values to all important predictors even if they are correlated, whereas cTree and cRF assess independent variable contributions (similar to partial correlations). In all 3 approaches, more populations were required to delist species that had more populations at listing (Fig. 1 & Supporting Information).

Previous abundances alone explained 63–68% of variance in proportion of historical populations required for delisting (Table 3), and all 3 modeling methods identified historical number of populations as the most important predictor (Fig. 2 & Supporting Information). This relation may have resulted because the response variable included historical number of populations in its formulation. However, if other predictors were strongly associated with this criterion they would be significant in at least the conditional analyses. All methods indicated a smaller proportion of historical populations was required to delist species that historically had a greater number of populations. The cTree indicated on average 5.9 times the historical number of populations was required to delist species with ≤ 1 historical populations, and delisting criteria were lower than historical numbers for species that had > 7 historical populations (Fig. 2a). Of species that had ≤ 7 historical populations, those with only 1 historical population had the highest proportional delisting criteria (on average requiring 6 times the historical number of populations for delisting). The cTree also split by proportion of historical populations remaining at listing. For species with > 9 historical populations, a higher proportion of historical populations was required to delist species when $> 63.2\%$ of historical populations remained at listing than when a lower proportion remained (Fig. 2a). In summary, species that were more abundant at listing and less abundant before anthropogenic decline required proportionally more populations to be delisted.

Previous abundance alone explained none of the variance in total number of individuals required for delisting and $< 22\%$ of variance in number of individuals per population required for delisting (Table 3). This indicated the numbers of individuals at listing and when the plan was written were poor predictors of individual-based delisting criteria.

Traits as Predictors

Traits alone poorly predicted population-based delisting criteria, but they explained 45–58% of variance in total number of individuals required for delisting when Hawaiian species were included (Table 3).

For this delisting criterion, physiographic division was important in all modeling methods. More individuals were required to delist species from the Pacific Mountain System, Intermontane Plateaus, Interior Plains, Interior Plains/Canadian Shield, and Atlantic Plain divisions than species from the Appalachian Highlands, Appalachian Highlands/Interior Plains/Interior Highlands, Atlantic Plain/Appalachian Highlands/Interior Plains, and Hawaii and Pacific Islands divisions (Supporting Information). Within the latter group (which included primarily species from Hawaii), cTree also split by life-history duration; more individuals were required to delist annual and short-lived perennial species than perennial species. The cRF assigned high importance to life form; more total individuals were required to delist herbs and lichens than vines, subshrubs, shrubs, and trees (Supporting Information).

Previous Abundance and Traits as a Predictor

Due to missing data, models including both traits and abundances were built with smaller data sets than models including traits or abundances alone (Table 3). Data for all predictor variables were available for < 20 species when Hawaiian species were excluded, and the resulting models did not explain substantial variance in any delisting criteria (Table 3). Thus, below we focus on analyses that included Hawaiian species.

Models including both abundances and traits explained a higher percentage of variance in number of populations required for delisting than models that included abundances only (from 10–19% to 13–49%) (Table 3). Number of populations at listing was an important predictor in all modeling methods, and number of populations when the plan was written also had high importance values in RF and cRF (Supporting Information). Reproductive mode was a splitting variable in cTree and had a moderate importance value in cRF. The cTree indicated fewer populations were required to delist species with ≤ 8 populations at listing and those with both clonal and sexual reproductive modes than species with > 8 populations at listing and with sexual reproduction only. These results were corroborated by the cRF partial dependence plot. The RF indicated more populations were required to delist monocarpic than polycarpic species (Supporting Information).

When recovery criteria were expressed as proportion of historical populations required for delisting, including both abundances and traits decreased the percentage of variance explained by cTree and cRF (from 62% to 32% and 36% to 33%, respectively) but increased the variance explained by RF (from 52% to 65%) relative to including abundances only (Table 3). The large decrease in model accuracy of cTree when traits were included and low accuracy of the traits-only models suggest traits explained little or no variation in this criterion.

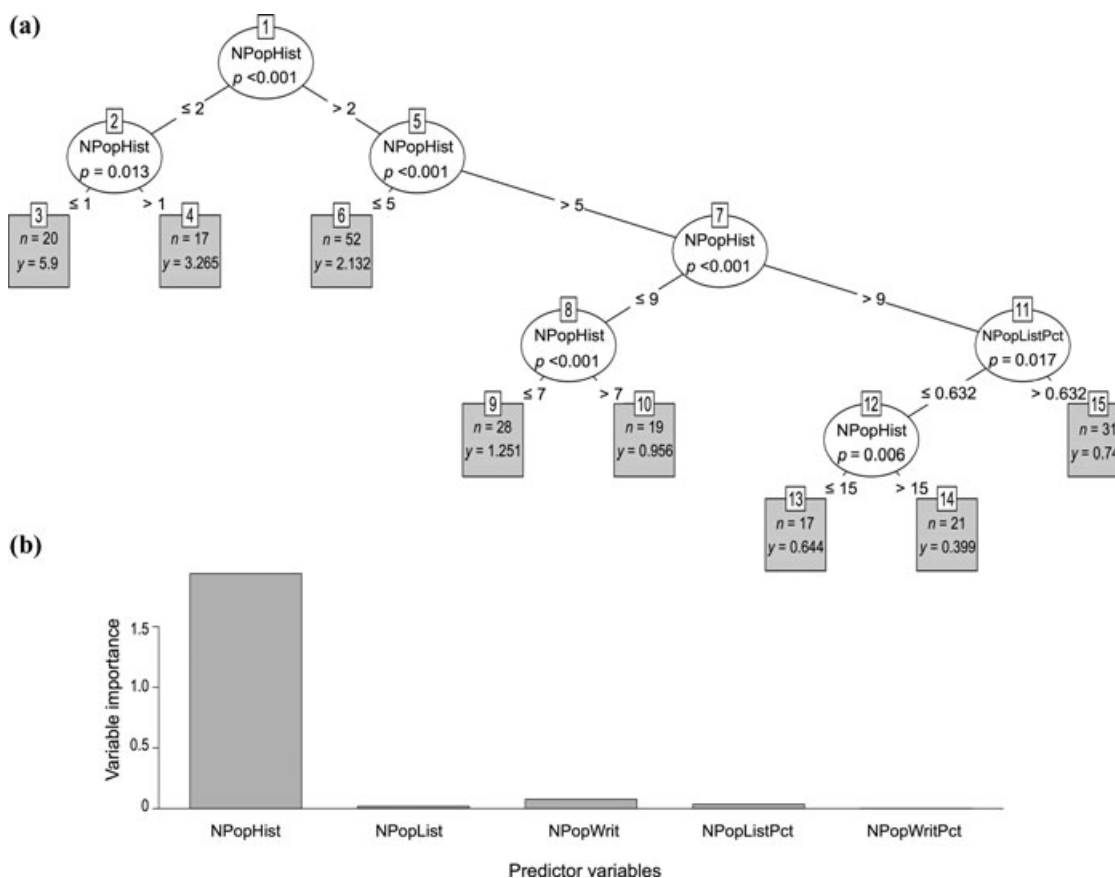


Figure 2. Results of analysis of the proportion of historical populations required for delisting under the U.S. Endangered Species Act on the basis of previous abundance (NpopListPct, proportion of historical populations remaining at time of ESA listing; NpopWritPct, proportion of historical populations remaining when recovery plan was written; see Fig. 1 for other abbreviations) as predictor variables and including Hawaiian species ($n = 205$): (a) conditional inference tree (shows how important predictor variables divide species into groups with similar response values) and (b) variable importance values from conditional random forest analysis measured as the mean increase in model error (units are proportion of historical populations) when each predictor variable is randomly permuted.

When the recovery criterion was total number of individuals, including both previous abundance and traits decreased the percentage of variance explained by cTree and cRF (from 56% to 54% and 41% to 31% respectively) but greatly increased variance explained by RF (35% to 56%) relative to traits only (Table 3). The effects of traits were similar between the 2 models, and we present results from the traits and abundances model to show the effects of abundances. All 3 methods identified physiographic division as an important predictor (Fig. 3 & Supporting Information). The cTree and RF indicated more individuals were required to delist species in the Pacific Mountain System, Intermontane Plateaus, Atlantic Plain, and Interior Plains divisions than species in other divisions, and cRF showed the same trends for these divisions except Interior Plains. The cTree and cRF further indicated that fewer individuals were required to delist species in the Atlantic Plain/Appalachian High-

lands/Interior Plains and Hawaii and Pacific Islands divisions than species in other divisions. The cTree also split by number of individuals at listing: 23,200 individuals were required on average to delist species with >3000 individuals at time of listing (Fig. 3a). The RF and cRF also indicated more individuals were required to delist species that had more individuals at listing and when the plan was written (Supporting Information). Duration was a splitting variable in cTree; more individuals were required to delist annual and short-lived perennial species than perennial species in the Atlantic Plain/Appalachian Highlands/Interior Plains and Hawaii and Pacific Islands divisions. Life form had a high variable importance value in cRF; more individuals were required to delist herbs and lichens/mosses than shrubs and vines, and the fewest individuals were required to delist shrubs and trees (Supporting Information).

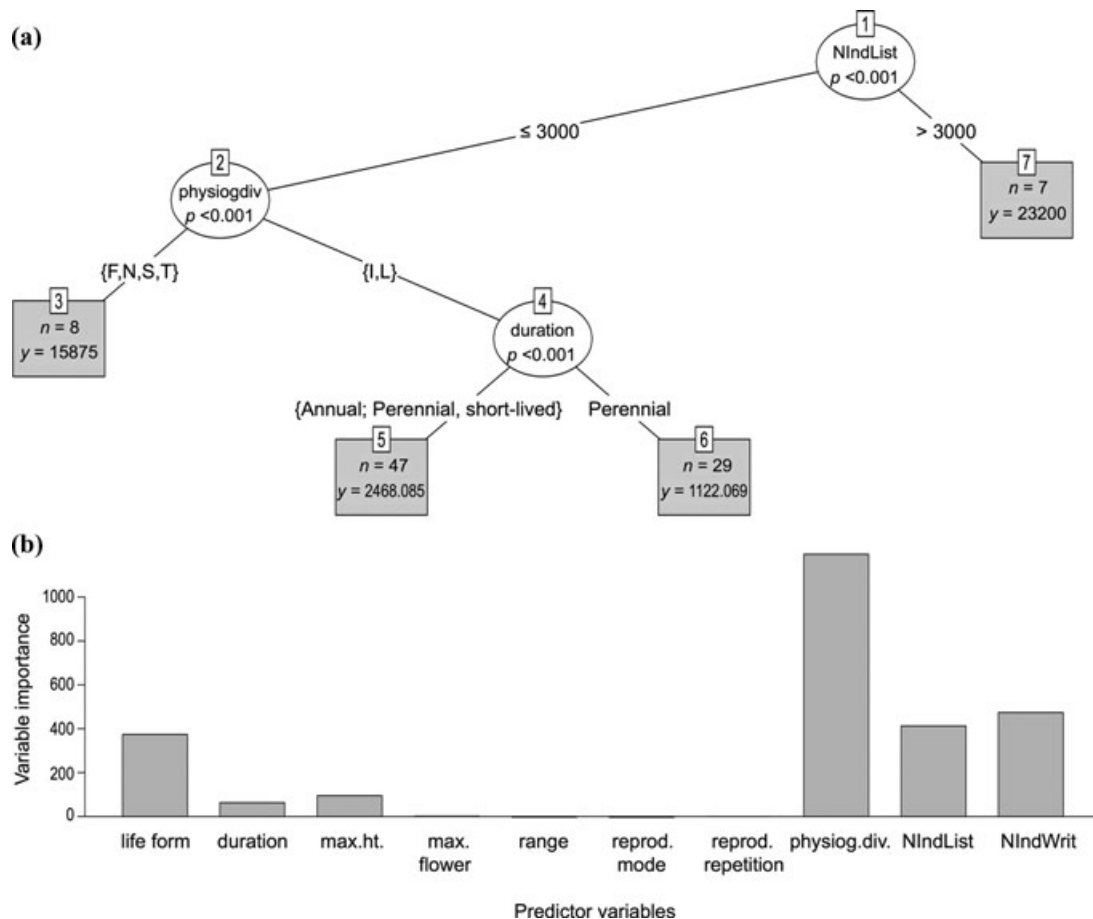


Figure 3. Results of analysis of the number of total individuals required for delisting under the U.S. Endangered Species Act (ESA) on the basis of distribution and biological traits (life form; duration, life-history duration; max.ht., maximum plant height; max.flower, maximum flower size; range; reprod.mode, reproductive mode; reprod.repetition, reproductive repetition; physiogdiv, physiographic division: F = Atlantic Plain, N = Interior Plains, S = Intermontane Plateaus, T = Pacific Mountain System, I = Atlantic Plain/Appalachian Highlands/Interior Plains, L = Hawaii and Pacific Islands) and previous abundance (NIndList, number of individuals at time of ESA listing; NIndWrit, number of individuals when plan was written) as predictor variables and including Hawaiian species ($n = 91$): (a) conditional inference tree (shows how important predictor variables divide species into groups with similar response values) and (b) variable importance values from conditional random forest analysis measured as the mean increase in model error (units are number of individuals) when each predictor variable is randomly permuted.

The previous abundance and traits model explained the highest overall percentage of variance in number of individuals per population required for delisting (approximately 20–48%) (Table 3), and physiographic division was important in all modeling methods (Supporting Information). The cTree showed more individuals per population were required to delist species from the Interior Plains and Pacific Mountain System divisions than from Atlantic Plain, Atlantic Plain/Appalachian Highlands/Interior Plains, and Intermontane Plateaus divisions, which in turn required more individuals than species from Hawaii and Pacific Islands (Supporting Information). The RF indicated more individuals per pop-

ulation were required to delist species from the Atlantic Plain, Interior Plains, Pacific Mountain System, and Intermontane Plateaus divisions. The cRF showed the same trends for these divisions, except Atlantic Plain, and further indicated fewer individuals per population were required to delist species in the Atlantic Plain/Appalachian Highlands/Interior Plains and Hawaii and Pacific Islands divisions. The RF and cRF indicated more individuals per population were required to delist species that had more individuals when the plan was written and at listing. Duration was a splitting variable in cTree; more individuals per population were required to delist annual and short-lived perennial species than perennial species in the

division of Hawaii and Pacific Islands. However, duration had low importance values in RF and cRF (Supporting Information).

Discussion

Our major finding, that delisting criteria were related primarily to prior abundance, is consistent with the results of Elphick et al. (2001) for birds and of Schemske et al. (1994) for a smaller number of plant species. We found more populations were required to delist species that had more populations at listing. Furthermore, proportionally more populations were required to delist species with fewer historical populations, a comparison not made by previous researchers. Delisting criteria that were based on individual abundances were also predicted by numbers of individuals at listing and when the plan was written, but only when both traits and abundances were included in the models. Numbers of individuals required for delisting were best predicted by the physiographic division in which the species occurs and by life form and life history duration in some models (Fig. 3 & Supporting Information). However, duration was only important within groups composed of Hawaiian species for which one delisting criterion was set for short-lived perennials and a lower criterion was set for long-lived perennials.

Importance of physiographic division in predicting individual-based recovery criteria may have been driven by differences in biology of plants in different divisions, different land-use patterns, or the interaction of both factors. For example, divisions associated with higher delisting criteria (Interior Plains, Intermontane Plateaus, and Pacific Mountain System) tend to have a greater proportion of public land, which is subject to land uses that alter carrying capacity but is less threatened by uses that cause permanent conversion of habitat (e.g., residential, agriculture, or industrial development), than the eastern United States (Flather et al. 1998). Range and abundance of listed plant species in the interior and western divisions have declined less than those of species in other areas (Leidner & Neel 2011). A lower probability of land conversion and smaller population declines increase recovery potential in these divisions because a larger proportion of the historic habitat and range remains and can support more individuals (Kerr & Deguise 2004). The Hawaii and Pacific Islands division was associated with low species delisting criteria, potentially because this division is severely affected by habitat loss and degradation and supports species with naturally limited distributions and specific habitats. Thus, these patterns may reflect what is possible for conservation in each region rather than biological mechanisms.

Differences between physiographic divisions may also have resulted from the particular species representing each division in our data set. The Atlantic

Plain/Appalachian Highlands/Interior Plains division, which was consistently associated with low species delisting criteria, was represented only by the broadly distributed but locally rare species *Isotria medeoloides*. The recovery criterion for this species of permanently protecting 75% of known populations and increasing abundances in 25% of populations translates to delisting when 2420 total individuals are conserved (U.S. Fish and Wildlife Service 1992).

Dependence of recovery criteria on prior abundances has been considered problematic because such criteria do not reflect species biology (Schemske et al. 1994; Elphick et al. 2001). We contend that relations between recovery criteria and previous abundance do not necessarily indicate recovery criteria are poorly formed and offer several explanations for the failure to detect relations between traits and recovery criteria.

First, lack of relations between traits and recovery criteria may be due to the traits we examined. Although we evaluated a larger set of traits related to persistence and more species than have been evaluated previously, different variables may yield significant associations. Basic life-history data are unavailable for most endangered plant species, which precludes more extensive analyses. Alternatively, the assumption that species with similar biological traits should have roughly equivalent extinction risks, and therefore similar criteria, may be faulty. Attempts to link life-history traits to rarity (Bevill & Louda 1999; Murray et al. 2002) and extinction risk (Traill et al. 2007; Brook et al. 2008) have not yielded consistently strong relations. For example, biological traits explained 0–13% (Sodhi et al. 2008) and 25–38% (Cardillo et al. 2008) of the variation in extinction risk for plants and mammals, respectively. Our traits-only models explained 0–21% and 0–58% of variation in number of populations and number of individuals required for delisting, respectively. Minimum viable population sizes were also not correlated with biological characteristics that affect general extinction vulnerability (Reed et al. 2003; Brook et al. 2006; Traill et al. 2007).

This lack of association may result if biological traits do not inherently increase or decrease risk but instead affect the way extinction risk is manifested. For example, body size in mammals is commonly thought to be correlated with extinction risk. In fact, this relation is contingent on factors such as range size and habitat type; thus, larger mammals may have higher or lower extinction risk depending on the context (Davidson et al. 2009). In declining plant populations, species capable of selfing are more likely to be affected by inbreeding depression, whereas obligately outcrossing species may experience Allee effects due to fewer compatible mates, but neither mating system is inherently more extinction prone or warrants higher recovery criteria.

Weak associations may also emerge because extinction risk and conversely recovery potential depend on unique

combinations of biological factors (e.g., body size, life history, and genetic diversity), ecological characteristics (e.g., habitat specialization, successional status, and range size), and anthropogenic factors (e.g., magnitude and duration of reductions in range or abundance) (Isaac & Cowlshaw 2004; Sanderson 2006; Lee & Jetz 2010). For example, habitat specialization can increase extinction risk (Brook et al. 2008), but its consequences only manifest when that habitat is highly altered (e.g., Farnsworth & Ogurcak 2008). Effects of intrinsic factors determining local demographic processes can be orders of magnitude smaller than (e.g., Collen et al. 2011) and counteracted by (Brook et al. 2006; Traill et al. 2007; Flather et al. 2011) large-scale, systematic threatening processes that cause regional or global declines. Furthermore, relative contributions of various intrinsic versus extrinsic factors and their interactions on extinction risk vary across species and contexts (Murray et al. 2002; Cardillo et al. 2008). Thus, although extinction risk is related to biological traits, its manifestation may be so highly contextual and singular that generalities are precluded. Consequently, recovery criteria that are similar in absolute magnitude may not yield equivalent magnitudes of risk reduction across species. An abundance that is more than sufficient for recovery of a species facing one set of threats could be woefully inadequate for biologically similar species in different threat contexts.

Additional variation arises from different interpretations of the meaning of *recovery* due to the vague terminology in the ESA (Goble 2009; Neel et al. 2012). Species can be delisted when they are no longer likely to be “in danger of extinction” or to become so “in the foreseeable future;” neither of these phrases is well defined. Interpretations of ESA recovery may range from barely exceeding minimum viable population size (Shaffer 1981), to reliance on continued management (Scott et al. 2010), to self-sustaining populations, to populations that are ecologically functional and evolutionarily viable (Sanderson 2006; Scott et al. 2010; Redford et al. 2011). This spectrum represents decreasing degrees of the “danger of extinction” over increasing periods of the “foreseeable future.”

Consequently, recovery criteria are highly normative and influenced by societal values, political will, and competing economic pressures in addition to biological requirements (Vucetich et al. 2006; Wilhere 2008). The definition of *recovery* used for any particular species is a combination of biology and political reality and reflects the balance between what is necessary and what is possible. As Elphick et al. (2001) noted, increasing transparency of the relative influence of biology and politics is essential for improving recovery plans.

Given the lack of evidence for strong correlations between traits and endangerment and the biological reasons why such associations may not exist, it is unclear what consistent and scientifically based criteria would

be. On one hand, correlation between abundances at listing or when a plan is written and recovery criteria may indicate recovery-plan authors are relying more on what is possible than “... what is biologically necessary” (Elphick et al. 2001). On the other hand, we argue that observed correlations are not inherently unreasonable and do not preclude a scientific or biological basis to the criteria. In fact, it would be difficult to imagine no relation between recovery criteria and prior abundances because that would suggest presence of factors that affect species persistence but are not correlated to abundance. Abundances at listing and when a plan is written may actually reflect the summary effects of species biology and extrinsic threats on abundance and may be the only available data quantifying those effects. They also provide a starting point for recovery because those abundances represent endangerment and may serve as a minimum threshold for determining when a species is no longer endangered. In many cases the U.S. Fish and Wildlife Service considers those abundances sufficient for recovery once threats are abated (Neel et al. 2012).

Abundances before anthropogenic decline (e.g., what we termed historical) provide a particularly relevant benchmark for criteria because they allow estimation of the reduction in range, habitat area, or abundance that has occurred. Although restoring the historical range or abundance is not required for recovery, understanding the magnitude of losses and the relative increase in abundance represented by particular criteria may be as relevant as absolute numbers of populations or individuals in terms of ensuring persistence. Because species with smaller ranges and fewer populations before anthropogenic decline start out at higher risk of extinction than more widespread species, it would be justifiable to protect a larger proportion of their populations, and our results indicate this is indeed occurring. Increased proportional protection could achieve the same level of risk reduction as provided by protection of a smaller proportion of populations or range for more widespread species, although the absolute criteria should be larger for the latter species.

Although the need to have more empirically based recovery criteria is recognized (Tear et al. 1993; Schemske et al. 1994), context-dependent extinction risk and recovery potential continue to preclude establishing consistent recovery criteria, or even a way to determine whether criteria are consistent across species. Ideally, scientists and practitioners would determine an acceptable level of extinction risk for all species and then apply a science-based framework to translate that risk into quantitative recovery criteria for each species. Despite an excellent scientific foundation for understanding effects of life-history traits and external threats on relative extinction risk, methods for translating generalities to quantitative estimates are lacking. Population viability analysis (Shaffer 1981)

offers the only quantitative method for risk assessment, but even proponents of these models do not consider them suitable for setting specific conservation criteria (Crone et al. 2011). A fundamentally new approach needs to be developed that weaves together a number of related fields, typically treated separately (e.g., determination of broad-scale correlates of rarity, past extinction patterns, or turnover at small spatial scales; time series analyses; comparisons of traits in rare versus common or endangered versus secure species; and incorporation of stochastic processes), and thus integrates species biology, anthropogenic threats, and their interactive effects to comprehensively quantify extinction risk and develop criteria for its abatement.

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Supporting Information

Detailed results from the best-fitting models for predicting delisting criteria (Appendices S1–S6) are available online. The authors are solely responsible for the content and functionality of these materials. Direct queries (other than absence of material) to the authors.

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