

Short communication

Genetic factors are less considered than demographic characters in delisting species

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ABSTRACT

When recovery goals for threatened and endangered species have been reached, these species will be removed from lists of threatened species. The self-sustainability of delisted species depends on both demographic and genetic factors, while genetic factors are still not considered as an essential part of evaluation in delisting decisions. In this study, we checked if genetic factors were less considered than demographic characters in delisting decisions and the following post-delisting monitoring plans (PDMPs). We found that only 32.76% (19 of 58 decisions) delisting decisions contained genetic factors, with genetic variation being the most frequently mentioned genetic factor, whereas all delisting decisions considered demographic characters. Moreover, we detected an increasing trend of genetic factors being considered in delisting decisions over time, but this may just be the result of more available genetic data produced by conservation studies rather than a rising awareness of the importance of genetic factors in policy making of delisting decisions. Genetic factors were also overlooked in PDMPs with only two out of 29 PDMPs monitoring genetic factors. As the rapid development of conservation genomics, we addressed the application value of genomic data in delisting decisions and proposed a candidate genetic criterion that effective population size should be greater than 1000 to assess the successful recovery of an endangered species and self-sustainability of delisted species.

1. Introduction

The current species extinction rate is approximately 100–1000 times higher than that of the background rate, largely due to human activities (Ceballos et al., 2015; De Vos et al., 2015; Pimm et al., 2014). To identify species for conservation priority, species are evaluated and classified into different categories based on their extinction risks. The species with high extinction risks are compiled in global and/or regional lists, such as the International Union for Conservation of Nature (IUCN) Red List of threatened species and Federal List of threatened or endangered species under the Endangered Species Act (ESA). Those lists have been widely used as key references in conservation studies, decision-making as well as conservation practices.

When recovery goals of a threatened or endangered species have been reached, it will be removed from lists of threatened species. Criteria for delisting are critical because far less attention and conservation efforts will be paid to a species once it is delisted. Population size is related to the local extinction risk because small-sized populations are susceptible to demographic factors (such as the Allee effect

and bottleneck effect due to catastrophes) and genetic factors (e.g., inbreeding depression and the accumulation of deleterious mutations) (Frankham et al., 2010; Lande, 1988). However, current assessments of delisting species usually only involve measurements of demographic characters. For example, IUCN (2012) uses population size and distribution range as key factors for category changes, such as removing species from threatened categories. In addition, the recovery goals of a threatened or endangered species for delisting in ESA predominantly comprise an increase in population size and the elimination or reduction of threats (Section 4 of the Endangered Species Act, <https://www.fws.gov/endangered/>).

Besides low immediate risks of extinction, a successful recovery of a threatened or endangered species also requires the ability to long-term self-sustain without human assistance. Although demography may have a more immediate effect than population genetics (Lande, 1988), genetic variation provides raw materials for natural selection and is, thereby, fundamental for species to adapt to changing environments. In addition, many species experience genetic deterioration during or before population decline (Spielman et al., 2004; Yang et al., 2018), but a

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rapid recovery of intraspecific genetic diversity hardly occurs when population size increases. Incorporation of demographic and genetic factors, thereby, has been recommended to assess the status of threatened and endangered species since the 1980s (Lande, 1988).

However, as genetic factors are not essential in delisting species, genetic information may be less considered in conservation activities. Only 38 cases of listing decisions made by US Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS) between 1996 and 2006 mentioned genetic information (Fallon, 2007). Pierson et al. (2016) reviewed 318 recovery plans of threatened species from the US, Australia, and five European countries, and found that less than half of these studies contain genetic information and/or suggest to collect it. Furthermore, in most of the recovery plans considering genetic information, measurements of genetic factors were only limited to within-population genetic variation and genetic structure, without testing other genetic factors that may affect the viability of populations/species, (e.g., inbreeding depression and gene introgression) (Pierson et al., 2016). Therefore, despite that there is a contradiction between the practical needs in conservation biology and the existing policy, it is still unclear whether genetic factors are receiving increasing concern in conservation practices related to delisting decisions and which genetic factors are prevalent to evaluate the potential of a species to adapt the ongoing environment changes.

In this study, we reviewed the proposals of delisting species from the Federal List of Endangered and Threatened Wildlife and Plants under ESA, and specifically aimed to answer the following questions: (1) whether genetic factors were generally less considered than demographic characters in delisting decisions; (2) if the proportion of delisting decisions including genetic factors increased over time; and (3) which genetic factor was the most frequently considered. In addition, we also analyzed available post-delisting monitoring plans (PDMPs) for delisted species to check how often the monitoring of genetic factors was suggested. Based on our results and the fast development of high-throughput sequencing techniques, we proposed a candidate criterion to evaluate successful recovery of threatened and endangered species and long-term maintenance of delisted species.

2. Materials and methods

2.1. Information source of delisted species

To obtain detailed information on delisting decisions, we searched the Environmental Conservation Online System (ECOS) (<https://ecos.fws.gov/ecp0/reports/delisting-report/>, accessed June 22, 2020), which provides information on delisted species by the U.S. Fish and Wildlife Service (USFWS), National Marine Fisheries Service (NMFS) and National Oceanic and Atmospheric Administration (NOAA), and downloaded final rule or proposed rule if final rule is not available for each of these delisting decisions. We only reviewed delisting decisions of the Federal List because no detailed decision proposals were available in IUCN although it also updates the status of listed species.

To refine our dataset for further analyses, we only selected proposals of delisting decisions following a successful recovery of target species (delisting can also be caused by extinction and errors in original records) by USFWS, NMFS and NOAA from 1978 (when the first delisting decision was made) to June 2020.

A PDMP is required by ESA for each delisted species due to recovery, and a relisting program will be initiated if there is evidence showing a delisted species fails to sustain itself during the PDMP. We therefore downloaded all available PDMPs for our selected delisting decisions from addresses provided in delisting rules to test whether the monitoring of genetic factors was prevalent, and a draft PDMP was used if we did not obtain the final version.

2.2. Demographic characters and genetic factors

Three demographic characters consisting of census population size, distribution range and/or occupancy area, and population trend were collected for each delisted species because of recovery. We chose these characters because large population size and wide distribution/occupancy area can reduce the adverse effects triggered by Allee effects and catastrophic events (Kramer et al., 2009), and population trend (declining, stable or increasing) is a key indicator reflecting population sustainability in the near future.

Seven genetic factors were collected and assigned into two categories as described by Pierson et al. (2016): (1) the general description of genetic composition comprising four genetic factors (i.e., genetic variation, gene flow, genetic structure, and effective population size); and (2) fitness-related parameters consisting of three genetic factors (i.e., inbreeding depression, hybridization and/or introgression, and outbreeding depression). Genetic variation is a direct index to reflect long-term sustainability of species, while gene flow, genetic structure and effective population size are related to the maintenance and accumulation of genetic variation (Charlesworth, 2009; Epps et al., 2005). Inbreeding, hybridization and outbreeding influence the viability of species by affecting the fitness of their offspring and their genetic integrity (Rhymer and Simberloff, 1996; Schierup and Christiansen, 1996).

2.3. Data analyses

To test whether genetic factors are overall less considered than demographic characters in delisting species, we calculated the proportion of delisting decisions, where a demographic character or genetic factor was measured, to the total selected delisting decisions (i.e., inclusion ratio). McNemar's test was used to examine the difference of inclusion ratio between demographic characters and genetic factors using R v3.4.3 (R Core Team, 2017). Furthermore, as there was only one delisting decision in some years (a total of 10 years, see Supplementary Table S1), we also checked the accumulative inclusion ratio, i.e. the proportion of accumulative delisting decisions that considered genetic factors to the accumulative total delisting decisions from 1985 (when the first delisting decision due to a successful recovery was made) to each following year with at least one delisting decision.

We then examined whether inclusion ratio varied among different taxon levels and between animals and plants. According to the definition of species by ESA, the term "species" in the Federal List includes three levels of taxa, i.e., species, subspecies, and DPS (distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature). Therefore, we allocated all target taxa involved in the selected delisting decisions into these taxa levels when calculating the inclusion ratio. In addition, we also divided all taxa into animals and plants, and calculated the inclusion ratio for each of these two species groups. Fisher's exact tests were used to test the difference in inclusion ratio among different taxa levels and between different species groups using R v3.4.3 (R Core Team, 2017).

To determine the most prevalent genetic and demographic factor considered in delisting decisions due to successful recoveries, the proportion of each genetic/demographic factor was calculated. In addition, to examine if genetic factors have been generally considered in the PDMPs, the inclusion ratio of genetic monitoring was calculated and compared with that of demographic monitoring.

3. Results

There were a total of 89 delisting decisions from the Federal List by June 2020, among which 11 (12.36%) were due to extinction, 20 (22.47%) were because of data errors and 58 (65.17%) were successful recovery cases (Fig. 1a). These successful recovery taxa were mainly at species level (including 31 species, 14 subspecies and 13 DPSs), and

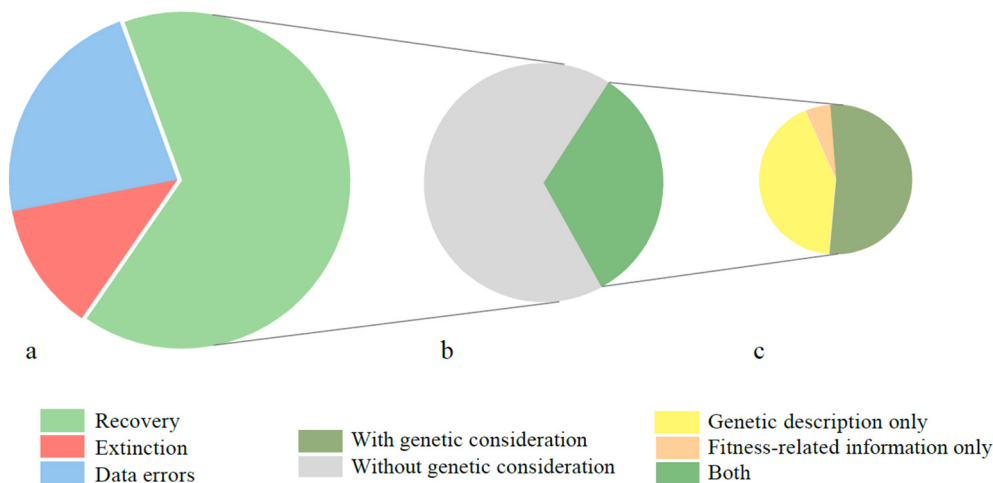


Fig. 1. Percentages of delisting reasons (a), whether or not considering genetic data (b) and which type data were considered (c) in delisting species from the Federal List of Endangered and Threatened Wildlife and Plants under ESA (<https://ecos.fws.gov/ecp0/reports/delisting-report/>, accessed June 22, 2020).

dominantly comprised animals (48 animal and 10 plant taxa). These 58 cases contained 57 final delisting rules and 1 proposed delisting rule.

Among these 58 delisting decisions, only one-third (32.76%, 19 of 58 decisions) mentioned genetic factors (Fig. 1b), whereas all of them (100%, 58 of 58 decisions) considered demographic characters (McNemar's $\chi^2 = 39.00$, $df = 1$, $p < 0.001$). Among the decisions mentioning genetic factors, ten decisions involved both genetic composition and fitness-related information, eight only included genetic composition information, and one only contained fitness-related information (Fig. 1c). Although the first delisting decision due to successful recovery was made in 1985, genetic factors were not considered until 2001. Since then, the accumulative inclusion ratio of genetic factors in delisting decisions has increased over time (Fig. 2).

The genetic inclusion ratio significantly varied among taxon levels (Fig. 3). The inclusion ratio at subspecies level (57.14%, 8 of 14 decisions) was significantly higher than that at the DPS level (7.69%, 1 of 13 decisions; Fisher's exact test, $p = 0.009$), and there was no difference in this index between species (32.26%, 10 of 31 decisions) and subspecies levels (Fisher's exact test, $p = 0.106$). Additionally, significant difference of inclusion ratio was not detected between species and DPS levels (Fisher's exact test, $p = 0.086$). Similar inclusion ratios were found in animals (14 of 48 decisions) and plants (5 of 10 decisions), with no significant difference (Fisher's exact test, $p = 0.181$) (Fig. 3).

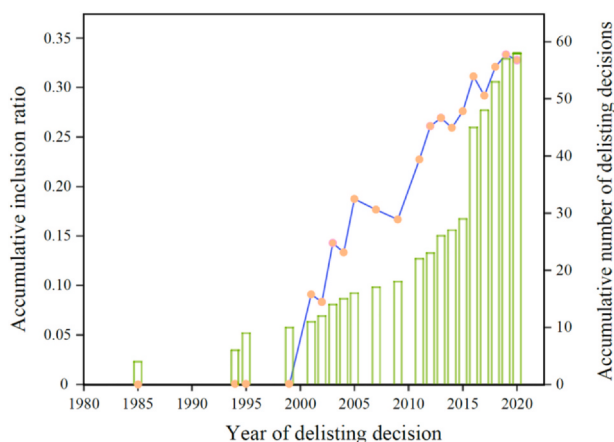


Fig. 2. The accumulative inclusion ratio of genetic factors in delisting decisions since 1985 when the first delisting decision was made following successful recovery. (Filled circle was used for accumulative inclusion ratio; bar was used for accumulative number of delisting decisions).

Among the delisting decisions due to successful recovery, genetic variation was the most prevalent genetic factor (29.31%, 17 of 58 decisions), followed by inbreeding depression and genetic structure (12.07%, 7 decisions for each genetic factor) (Fig. 4). Gene flow (10.34%, 6 decisions), effective population size (8.62%, 5 decisions), and hybridization and/or introgression (6.90%, 4 decisions) were less frequently considered in delisting decisions (Fig. 4). No delisting decisions considered outbreeding depression. For the three demographic characters, census population size was the most frequently considered character (94.83%, 55 of 58 decisions), followed by population trend (84.48%, 49 decisions) and distribution range and/or occupancy area (63.79%, 37 decisions) (Fig. 4). Therefore, the frequency of each demographic character considered in delisting decisions was far higher than that of any genetic factor, and the inclusion ratio of the most prevalent genetic factor was even lower than that of the least considered demographic character (McNemar's $\chi^2 = 13.33$, $df = 1$, $p < 0.001$) (Fig. 4).

Twenty-nine PDMPs were used in our study including 24 final versions and 5 draft versions. However, only 2 recently conducted PDMPs (*Vireo atricapilla* (delisting date 16 May 2018) and *Ursus americanus luteolus* (11 March 2016)) contained genetic monitoring, with an inclusion ratio of 6.90%, while all the 29 PDMPs set goals to collect demographic information (McNemar's $\chi^2 = 27.00$, $df = 1$, $p < 0.001$).

4. Discussion

Self-sustainability, which depends on both demographic and genetic characters, is the ultimate goal of biological conservation. Assessments only based on a census of a population may underestimate the extinction risk of threatened and endangered species, and incorporation of genetic factors ought to improve our prediction of sustainability (Frankham, 2003, 2005; Lande, 1988). However, our results revealed that the overall inclusion ratio of genetic factors was much lower than that of demographic information, and the inclusion ratio of the least considered demographic character was even higher than that of genetic variation, the most prevalent genetic factor. Moreover, genetic monitoring was overlooked in PDMPs, but all PDMPs suggested demographic monitoring. All these results showed that genetic factors were less considered compared with demographic characters.

The thought that demographic characters, especially population size, can reflect genetic information (Frankham, 1996; Leimu et al., 2006) may cause the less consideration of genetic factors in conservation activities. Nevertheless, an increase in population size is not equal to the recovery of genetic variation, as the accumulation of genetic

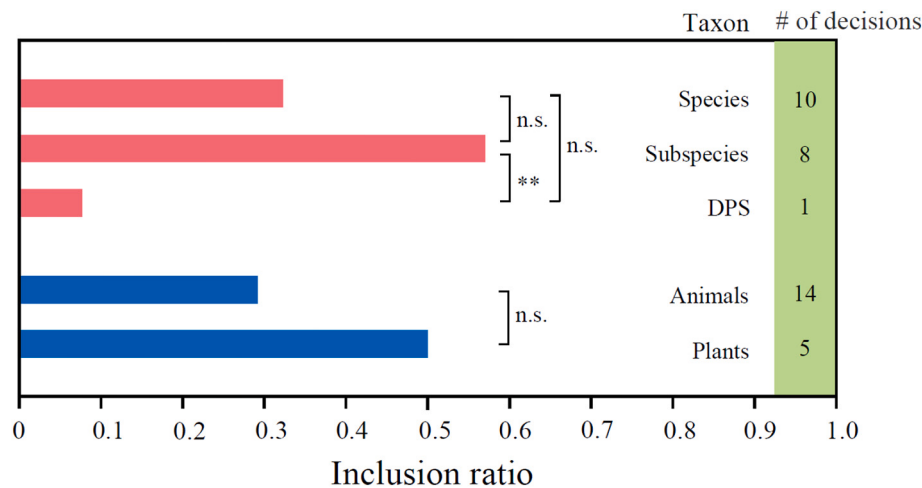


Fig. 3. The comparison of genetic factors considered in delisting among species, subspecies, and DPS (distinct population segments) and between animals and plants.

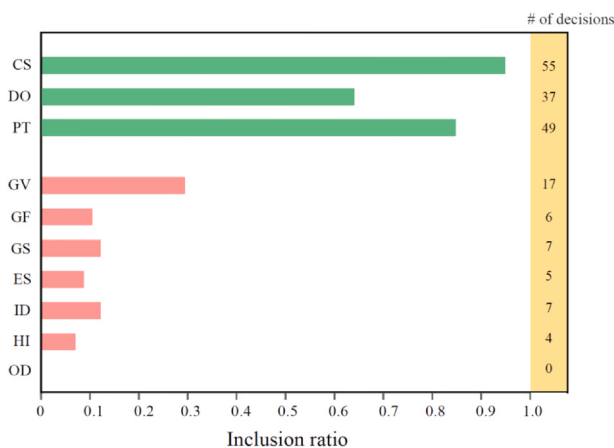


Fig. 4. The percentage of each demographic and genetic item considered in delisting decisions.

(Total number of delisting decisions used here is 58. The details about abbreviations are as follows: CS = census population size; PT = population trend; DO = distribution range and/or occupancy area; GV = genetic variation; GF = gene flow; GS = genetic structure; ES = effective population size; ID = inbreeding depression; HI = hybridization and/or introgression; OD = outbreeding depression).

variation relies on both population size and the number of generations (Nei et al., 1975). For example, low genetic variation was found in both wild and artificial populations of *Metasequoia glyptostroboides*, a living fossil endangered plant, despite a drastic increase in its population size owing to wide plantation, threatening the long-term maintenance of this species (Li et al., 2005, 2012). Similar to ESA, IUCN uses population trend, distribution range and number of mature individuals to classify endangered species (IUCN, 2012). However, a study on species of different endangered status in IUCN indicated that these characters were not well correlated with genetic diversity (Willoughby et al., 2015), further addressing the need of genetic criteria in making delisting decisions.

In addition to being indicators of genetic health of populations, changes in genetic parameters can also reflect population dynamics. Compared with traditional methods monitoring demographic characters, genetic monitoring is more cost-effective, more sensitive and more reliable (Schwartz et al., 2007). Moreover, monitoring using genetic factors can obtain past information of species using museum specimen, providing a remedial measure when investigation records are not available. Given the low inclusion ratio of considering genetic monitoring in PDMPs, we suggest ESA to pay more attention to survey

genetic factors after delisting.

It is gratifying that we detected a rising trend of considering genetic factors in delisting decisions. Such a trend is likely to result from the increasing number of genetic studies on threatened and endangered species due to academic concerns and development of techniques (Carvalho et al., 2019; Di Marco et al., 2017; Ouborg et al., 2010), and ESA collects all available information when making delisting decisions. Genetic factors were incorporated into studies of biological conservation since 1970s, and then had contributed greatly in many conservation practices such as defining management units and tracking illegal trades (Frankham et al., 2010; Mable, 2019). Nevertheless, as genetic criteria are absent, genetic factors may be overlooked in delisting decisions and PDMPs even when genetic data are available, leading to the overall low inclusion ratio of genetic factors in the existing delisting decisions and PDMPs and likely impeding the future applications of genetic factors in assessing the status of threatened and endangered species.

Although the most prevalent genetic factor considered in delisting decisions was genetic variation, it hardly mirrored the potential of a species to adapt to future environmental changes, restricting its contribution to guiding conservation activities, because very few molecular markers were used in a study (usually less than 15) and most types of molecular markers are not fitness-related (Kohn et al., 2006; Lu et al., 2006; Supple and Shapiro, 2018). The great improvement and the much decreased cost in high-throughput sequencing techniques have made it available to collect genetic information at the genomic level, providing mass data of genetic variation sufficient for comprehensive genetic evaluations of threatened and endangered species and initiating conservation genomics era (Corlett, 2017; Hayden, 2014; Ryder, 2005).

In addition to increasing the precision in measuring some traditional genetic factors like gene flow, inbreeding level and gene introgression, genomic data can offer explicit insights into the mechanisms related to adaptation, including whether a threatened or endangered species has accumulated more deleterious alleles than its closely related non-threatened species due to its extremely small population size (Yang et al., 2018). Genomic information has also been used to infer the roles of long-term historical events (e.g., Quaternary glacial period) and anthropogenic activities in the endangerment of studied species through detecting population dynamics from millions of years ago to the recent hundreds of years (Terhorst et al., 2017; Yang et al., 2018). Moreover, genomic data can be applied in other research fields, such as landscape genomics, providing new insights for species conservation studies by determining how species response in changing environments using methods like environmental association analyses (EAA) (Waldvogel et al., 2020).

For the convenience of making delisting decisions and the following

PDMPs, it is necessary to select a genetic factor that can represent the genetic status of species. Using genomic data, effective population size, which can reflect overall genetic variation, inbreeding level, genetic drift and fitness (Charlesworth, 2009), can be a candidate for evaluating the adaptive potential. Furthermore, the effective population size for a genetically healthy species has been generally considered as larger than 1000 (Frankham et al., 2014), which may become a criterion in delisting species and PDMPs, though there are debates regarding the detailed values (e.g., Flather et al., 2011; Franklin et al., 2014; Jamieson and Allendorf, 2012).

Benign human assistance is indispensable for seriously endangered species (Frankham, 2003), and precise status assessment is a key premise for appropriate allocation of conservation resources. Our results emphasized that genetic criteria based on genomic data must be made in delisting decisions and PDMPs, in case of the underestimation of species' endangerment. Moreover, we also suggested to consider genetic information in other stages of conservation activities, e.g., listing and designing recovery plans, for a comprehensive recovery of the potential to adapt to varying environments driven by global changes.

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CRediT authorship contribution statement

Chao-Nan Liu: Data curation, Formal analysis, Methodology, Visualization, Writing-Original draft preparation.

Yuan-Yuan Li: Formal analysis, Writing-Reviewing and Editing.

Rong Wang: Formal analysis, Methodology, Writing-Reviewing and Editing.

Xiao-Yong Chen: Conceptualization, Funding acquisition, Supervision, Writing- Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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