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RESEARCH ARTICLE

Evaluating the genome-wide impacts of species translocations: the greater prairie-chicken as a case study

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Abstract

A variety of conservation management strategies have been developed to address rapid, anthropogenically-driven biodiversity loss. The translocation of individuals from viable populations to those experiencing significant decline is one such strategy to increase genetic diversity and avoid extirpation, yet efficacy of this strategy has rarely been examined in detail utilizing genomic data. Here, we employ a conservation icon, the greater prairie-chicken (*Tympanuchus cupido pinnatus*), as a case study to demonstrate how genome-wide SNPs derived from RADseq offer the ability to assess translocation success with respect to the genomic aspects of genetic restoration, encompassing (1) the alleviation of inbreeding (2) the restoration of evolutionary potential, and (3) the maintenance of local variation. Genome-wide diversity estimates calculated from 356,778 SNPs demonstrate that translocations rescued the Illinois population from severe inbreeding and lack of genetic diversity, restoring variation to levels comparable to the three non-bottlenecked source populations. Delineation of genetic structure using non-linked and ubiquitously genotyped SNPs reveal distinct genetic variation among the source and recipient populations as well as high levels of admixture in the post-translocation population resulting from translocations. Estimated ancestry derived from private alleles uncover introgression of unique variation from each source population as well as the maintenance of substantial levels of variation unique to Illinois. Our findings demonstrate that genome-wide analysis of variation is a valuable management tool for measuring the genomic effects of translocations and, subsequently, gauging genetic restoration success.

Keywords Translocations · Conservation · Genetic restoration · Population genomics · RADseq · Greater prairie-chicken

Introduction

In the face of the Anthropocene, a wide array of conservation management practices have emerged attempting to mitigate accelerating rates of species loss and reverse population declines. Among these, species translocations, here defined as the human-mediated movement of individuals between wild populations, have become common practice (Fischer and Lindenmayer 2000; Morris et al. 2015; Brichieri-Colombi and Moehrenschlager 2016; Swan et al. 2016; Ralls et al. 2020). Translocation programs are often implemented by supplementing small, isolated populations with the goal of preventing extirpation through increasing population size and genetic diversity. This increase in genetic variation is intended to restore the genetic "health" of populations by alleviating inbreeding depression and increasing evolutionary potential while maintaining local adaptive variation, a process referred to as genetic restoration (Hedrick 2005).

While some translocations have prevented short-term extirpation, many have yielded equivocal results (Fischer and Lindenmayer 2000; Short 2009; Godefroid et al. 2011; Miskelly and Powlesland 2013; Morris et al. 2015; Whiteley et al. 2015; Brichieri-Colombi and Moehrenschlager 2016; Bubac et al. 2019). Ambiguous outcomes have largely been attributed to programs lacking consistent evaluation criteria

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for determining success or neglecting post-translocation monitoring altogether (Fischer and Lindenmayer 2000; Whiteley et al. 2015). Studies that do evaluate the effects of translocations often use demographic measures such as population growth rate to gauge success (Marshall and Spalton 2000; Ducatez and Shine 2019; Price et al. 2020), which may reflect temporary demographic expansion rather than increases in genetic diversity via successful introgression. Other studies focus on population genetic markers (e.g. microsatellites and mitochondrial DNA) as molecular surrogates of overall genomic diversity to assess changes in diversity, population structure, and levels of introgression following translocations (Leberg and Ellsworth 1999; Talbot et al. 2003; Arrendal et al. 2004; Bouzat et al. 2009; Epps et al. 2010; Pacioni et al. 2013; Bateson et al. 2014; Weise et al. 2020). However, these studies may be restricted by the nature of molecular variation (e.g. neutral vs. adaptive or molecular vs. quantitative), the limited representation of overall genomic diversity, and the need for assessing ecologically relevant measures of fitness (e.g. adaptive variation or inbreeding depression).

The advent of cost-effective reduced representation genomic techniques like restriction-site associated DNA sequencing (RADseq) offers those managing populations of conservation concern tools to assess the genomic effects of species translocations precisely and comprehensively. While these methodologies have seen widespread application (Andrews et al. 2016; Hoban et al. 2016; Moore and Benestan 2018), their direct implementation in assessing conservation-focused population management are less common. Here, we demonstrate the effectiveness of RADseq in detailing the efficacy of translocations in genetic restoration of an endangered wild population of greater prairie-chicken (*Tympanuchus cupido pinnatus*), a conservation icon that pioneered studies on the genetic effects of demographic bottlenecks and genetic rescue.

During the second half of the twentieth century, Illinois witnessed the near extirpation of the greater prairie-chicken as a result of severe habitat loss and fragmentation. Estimated at around 2 million individuals state-wide in the early 1800s, populations had contracted to approximately 2000 individuals among 179 localized groups in 1962 and by 1992 just 46 birds remained in two isolated populations in Japer and Marion counties. This severe population bottleneck was accompanied by reductions in fitness, with significant declines in both egg fertility (19% reduction overall) and success (i.e. proportion of hatched fertile eggs; 25% reduction overall) observed between 1963 and 1991 (Westemeier et al. 1991, 1998). In an attempt to interrupt the inexorable extinction vortex, greater prairie-chickens were translocated from larger populations in Minnesota, Nebraska, and Kansas populations between 1992 and 1998, which lead to temporary increases in population size and fitness (Bouzat et al. 1998a). The genetic consequences of the translocations into the Jasper County population were evaluated using nuclear microsatellite markers and a hypervariable control region of mitochondrial DNA. As expected, measures of genetic diversity for both marker types showed increased diversity in the Illinois population following the translocations. However, changes in diversity estimates from microsatellites lacked statistical significance (Westemeier et al. 1998; Bouzat et al. 2009).

In this study, we utilized RADseq to document the genomic impacts of translocations on the greater prairie-chicken population in Jasper County, Illinois by measuring changes in genome-wide variation in relation to source population diversity. We delineated differences in genomic variation among source and recipient populations by evaluating patterns of pairwise differentiation and population structure. Moreover, the identification of private alleles among populations provided the opportunity to track the introgression of foreign alleles and persistence of local alleles in the post-translocation population, and thus estimate relative levels of ancestry from the recipient and source populations. Results from this study demonstrate that genomic assessment of intraspecific translocations utilizing RADseq loci facilitates the investigation of all major facets of genetic restoration (sensu Hedrick 2005), including (1) the alleviation of inbreeding for short-term viability, (2) the restoration of overall genomic diversity for long-term viability, and (3) the persistence of local diversity. Our study further illustrates how the breadth and precision afforded by genomic technologies allows conservation biologists and mangers to define and comprehensively evaluate the success of species translocation programs.

Methods

Population sampling and DNA extraction

This study is based on genome-wide sampling of 101 individuals collected from 5 populations of greater prairie-chicken. Samples from the Illinois focal population included pre-translocation ($n=7$; 1974–1991; ILPRE) and post-translocation samples from Jasper County collected 7 years following the completion of translocations ($n=23$; IL2003). Source population samples included those from Kansas ($n=21$; KS1999), Nebraska ($n=25$; NE1993), and Minnesota ($n=25$; MN1992). Source population samples were taken during or within 2 generations of translocations from their respective populations. All DNA samples were extracted from blood collected from adult prairie-chickens of both sexes. Methods for DNA extractions for the Illinois and Kansas populations are described elsewhere (Bouzat et al. 1998b; Johnson et al. 2003, 2007). DNA from blood samples

collected from Minnesota and Nebraska was extracted with DNeasy blood and tissue kits using 50 µL aliquots of blood. DNA quantity was measured using a Qubit 3.0 Fluorometer with Qubit dsDNA Broad Range and High Sensitivity Assay kits. All DNA concentrations were normalized to 12 ng/µL when possible using 10 mM Tris–Cl and 0.5 mM EDTA.

ddRAD library preparation and sequencing

Libraries were prepared and sequenced by Texas A&M Genomics and Bioinformatics Services using a modified version of the double-digest restriction-site associated DNA sequencing (ddRAD) protocol by Peterson et al. (2012) using 100 ng of DNA per sample. Individual DNA samples were digested using restriction enzymes PstI and MboI. Each sample was ligated to a combination of one of 48 unique P5 barcodes and one of 4 unique Illumina-compatible P7 sequences. Following digestion and ligation, individual samples were multiplexed into 4 separate libraries and purified using Qiagen PCR Purification columns. Size selection was performed on individual libraries using Pippin Prep targeting 280–500 bp fragments. Each library of selected fragments was separately amplified using 18 PCR cycles during which a standard Illumina multiplexing read index was incorporated using Phusion Hi-Fidelity Taq (NEB). PCR products were then cleaned using Qiagen PCR purification columns and 1X AMPure XP beads, followed by quantification and quality assessment on a Fragment Analyzer (Advanced Analytics). Completed libraries were further multiplexed into a single library and sequenced on two lanes of the Illumina NovaSeq 6000 S2 using 2 × 150 paired-end reads. Due to low read coverage, 3 of the 7 ILPRE samples were supplemented with additional reads from duplicate samples (see Supplementary Materials Sect. 1 for details).

ddRAD loci assembly

Read quality filtering and demultiplexing

Initial read quality filtering was performed using FastQC v0.11. Reads were further filtered by the *process_radtags* program of Stacks v2 (Rochette et al. 2019), whereby those containing ambiguous barcodes, ambiguous cut-site sequences, or a mean Phred score of ≤ 10 (within a sliding window spanning 15% of the read length) were removed from further analysis. Following quality filtering, *process_radtags* demultiplexed reads into their corresponding individual samples.

De novo assembly and SNP filtering

Reads were assembled into loci using the *denovo_map.pl* pipeline of Stacks v2.41 (Rochette et al. 2019). The *ustacks* parameter values for minimum stack depth (*m* parameter), mismatches per locus within an individual (*M* parameter), and mismatches between loci of different individuals within *cstacks* (*n* parameter) were tested following methods described in Rochette & Catchen (2017) using a subset of 14 random individuals from across all populations. Final values of $m = 3$ and $M = n = 4$ were found to be most appropriate for this dataset. Due to the extremely large number of cut sites per individual, genotypes and SNPs within *gstacks* were called using a minimum significance value of 0.01 (gstacks-*gt-alpha 0.01*) for high confidence in nucleotide calls in the final set of loci. Loci were exported using the *populations* program of Stacks v2.41 (Rochette and Catchen 2017). For a locus to be considered for downstream analysis, it was required to be present in at least 80% of a given population (*r* parameter). In order to limit the number of false-positive SNP calls due to PCR duplication and/or sequencing errors, a minimum allele frequency filter of 0.02475 (*-min-maf* option), calculated using methods described in Rochette & Catchen (2017), was also applied (see Table S1, "Full" dataset). Reads were also assembled using the *ref_map.pl* pipeline of Stacks v2.41 utilizing the greater prairie-chicken genome assembly (GenBank: MOXI01000000) for comparison (see Supplementary Materials Sect. 2 for more details). Due to analogous patterns of genomic diversity, population structure, and private alleles in conjunction with higher mean locus coverage, we chose to perform analyses with de novo-produced loci.

Genome-wide diversity and population differentiation analyses

Measures of population-level genomic diversity, including observed (H_o) and expected (H_e) heterozygosity, nucleotide diversity (π), and inbreeding coefficients (F_{IS}), were calculated within the *populations* program of Stacks. Confidence intervals (99%) for mean diversity estimates were calculated by 1,000 bootstrap replicates across SNPs using the r package boot (R Core Team 2013; Canty and Ripley 2013). To test if mean genomic diversity measures significantly differed between populations, pairwise Wilcoxon rank sum tests were performed with Bonferroni correction for every combination of populations across all measures of genomic diversity. Mean SNP-based (F_{ST}) and haplotype-based (F_{ST}' and Φ_{ST}) measures of pairwise differentiation were calculated within *populations* (*-fstats* option) and corresponding standard errors were calculated by hand using r (R Core Team 2013). To determine if a substantial number of SNPs could erroneously influence differentiation estimates, deviation from Hardy–Weinberg was tested for among all SNPs using VCFtools v0.1.16 (Danecek et al. 2011). Further, differentiation estimates were calculated again after removing all but one SNP per RAD locus (*-write-single-snp* Stacks

option) to identify whether known linkage disequilibrium distorted patterns of differentiation. In order to ensure patterns of genomic diversity and pairwise differentiation were not heavily biased due to differences in the number of loci per population, *populations* was run a second time incorporating an additional filter requiring loci to be present across all populations ($p = 5$; Table S1, "Shared loci" dataset). Results were also checked for bias due to differences in number of individuals sampled per population by randomly subsampling 7 individuals (i.e. the smallest population sample size) from each source population (KS1999, NE1993, and MN1992) and IL2003 (Table S1, "Subsampled" dataset; see Supplementary Materials Sect. 3 for more details).

Population structure analyses

Principal component analysis

We assessed relative patterns of population structure among source, recipient, and post-translocation populations by performing principal component analysis (PCA). To reduce the possibility of linked SNPs heavily influencing clustering patterns of the PCA, the *populations* program from Stacks v2.41 (Rochette et al. 2019) was run requiring loci to be present across all populations and including only one SNP per RAD locus (*-write-single-snp* parameter, Table S1, "single SNP" dataset). Two PCAs were performed using the ade4 package (Dray et al. 2020) in R: (1) including source populations (KS1999, MN1992, and NE1993) and the Illinois pre-translocated population (ILPRE); and (2) comprising all populations, including the Illinois post-translocated population (IL 2003). The proportion of variation explained by PC1 and PC2 were calculated using the r package factoextra (Kassambara and Mundt 2020).

Structure analysis

To quantify population structure as well as characterize admixture in the post-translocation population, we performed cluster analysis using Structure v.2.3.4 (Pritchard et al. 2000). Structure uses multi-locus genotype data and Bayesian model-based clustering methods for characterizing distinct genetic populations and identifying admixed individuals within sample groups. Runs in Structure were implemented using the Admixture model with the assumption of correlated allele frequencies among populations due to shared ancestry (Ross et al. 2006; Johnson et al. 2007). Runs were performed with 10 iterations per value of K for $K = 1$–7, each with a burn-in period of 5,000 replications and 10,000 MCMC replications. Due to uneven sample sizes among populations, the most likely value for K was determined using the estimators MedMeaK, MedMedK, MaxMeaK and MaxMedK proposed by Puechmaille (2016), calculated using StructureSelector (Li and Liu 2018). Consensus plots of the major mode of clustering were generated for each value of K using the main pipeline of CLUMPAK (Kopelman et al. 2015), which employs CLUMPP (Jakobsson and Rosenberg 2007) to find shared clustering patterns among individual runs of each K value.

Private allele analyses

Identification of private alleles among the pre-translocation and source populations (ILPRE, KS1999, NE1993, and MN1992) and their subsequent detection following the translocations in IL2003 was conducted using a custom script (https://doi.org/10.5281/zenodo.3926999). Briefly, *populations* was run using the filtered SNPs from the "shared loci" dataset (Table S1) as a whitelist (*-W* option) on all populations save IL2003 to ensure private alleles were coded correctly in the resultant summary statistics output file (population.sumstats.tsv). We then generated a distribution of the number of private alleles found among KS1999, NE1992, MN1992, and ILPRE. Private allele loci were then backreferenced to the original "shared loci" dataset run of *populations*, which provided genotyping of the IL2003 population, to detect which private alleles were present in the IL2003 population.

The distribution of private alleles among IL2003 individuals was generated using a combination of a custom script (https://doi.org/10.5281/zenodo.3927011), VCFtools v0.1.16 (Danecek et al. 2011), and Microsoft Excel (2019). To decrease potential bias due to sample size, we normalized raw counts of private alleles by the total number of private alleles detected within the respective population from which they originated (i.e. ILPRE or one of the source populations). In order to generate an inferred ancestry for each IL2003 individual, we converted each normalized count into a proportion of the individual's total ancestry (i.e. sum of all normalized counts).

Results

After initial quality filtering, we retained 948,296,700 reads with a mean of 8,318,392 reads per individual (standard error = 235,972). The initial de novo assembly (Table S1, "Full" dataset) generated 137,132 loci containing 356,788 SNPs with a mean depth of 21.4X per site per individual ($SD = 16.9$). After reducing loci to only those sampled across all populations and eliminating known linked SNPs (Table S1, "Single SNP" dataset), a total of 25,324 loci

containing 15,530 SNPs remained with a mean depth of 34.7X per site per individual ($SD = 15.6$).

Genomic diversity point estimates

Analysis of mean genomic diversity revealed that, prior to the translocations, the Illinois population (ILPRE) had significantly reduced diversity compared to the non-bottlenecked source populations across all measures (Fig. 1). The ILPRE population had considerably lower heterozygosity (H_o and H_e) and nucleotide diversity as well a substantially higher inbreeding coefficient (F_{IS}) compared to source populations. All measures of diversity between ILPRE and individual source populations were significantly different ($P < 0.001$; Table S2.1). When compared to the average value of the three source populations, the magnitude of ILPRE's reduced diversity was consistent across estimates of heterozygosity (H_o and H_e) and nucleotide diversity, ranging from a reduction of 16% to 23%. The most marked difference among diversity measures between ILPRE and the source populations was revealed by the inbreeding coefficient; ILPRE was the only inbred population ($F_{IS} > 0$) and had an inbreeding coefficient more than threefold higher than the average of the three source populations. These patterns held when controlling for both differences in the number of loci per population as well as differences in the number of sampled individuals per population (Figure S1 and Tables S2.2 & S2.3).

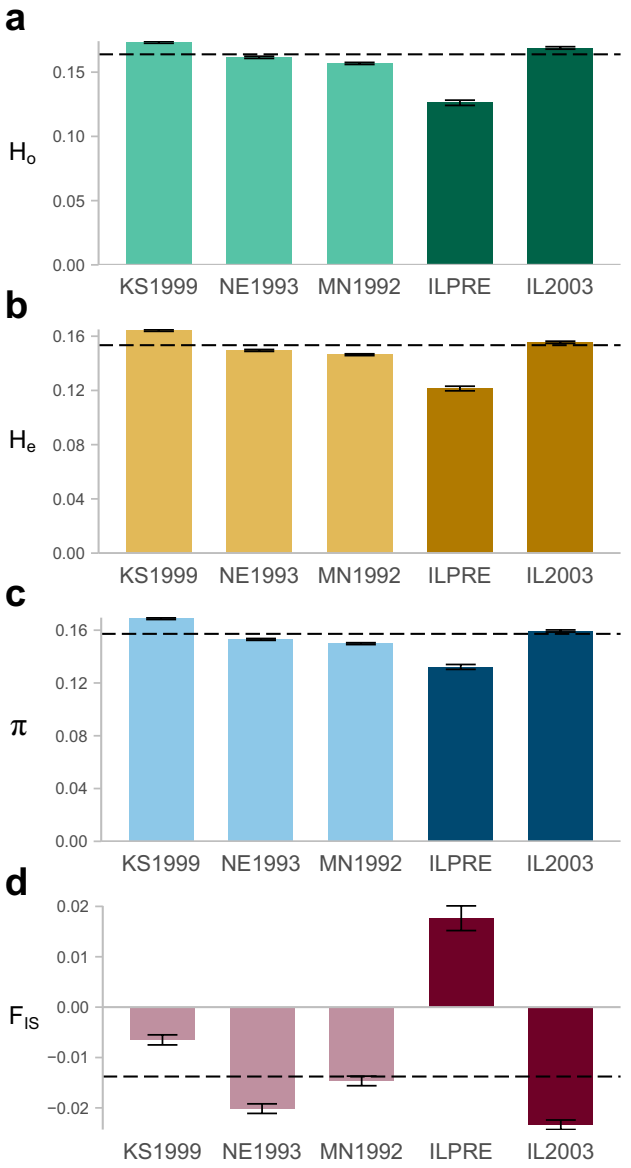

Fig. 1 Population-level point estimate means of genomic diversity using the "full" dataset of SNPs ($n = 356{,}778$) with 99% confidence intervals of the Illinois population prior to (ILPRE) and after (IL2003) translocations compared to the source populations (KS1999, NE1993, MN1992). Measures of genomic diversity include (**a**) observed heterozygosity, (**b**) expected heterozygosity, (**c**) nucleotide diversity, and (**d**) inbreeding coefficient. Dashed lines represent the average of the source population (KS, MN, and NE) point estimate means for each measure

Seven years following the translocation of 271 individuals into Jasper County, Illinois, the population (IL2003) retained a pronounced increase in genomic diversity across all measures ($P < 0.001$; Fig. 1 and Table S2.1). In comparison to estimates preceding the translocations (ILPRE), IL2003 had significantly higher heterozygosity (34% and 28% higher for H_o and H_e, respectively) and nucleotide diversity (21% higher), and nearly a 3.5-fold reduction in F_{IS}. Further, all estimates of genomic diversity for the post-translocation IL2003 population were either comparable to or surpassed the average of all source populations. These patterns held when controlling for differences in the number of loci per population and differences in the number of sampled individuals (Figure S1 and Tables S2.2 & S2.3).

Population differentiation

Relative patterns of pairwise population differentiation were consistent across all measures (Φ_{ST}, F_{ST}, F_{ST}'; Table 1, S3.1, & S3.2, respectively). For the most part, comparisons that showed the highest level of differentiation were those between ILPRE and the source populations. Following the

Table 1 Population pairwise Φ_{ST} (above diagonal) represented with a relative heat map (red = highest value, white = lowest value) and corresponding standard errors (below diagonal)

	ILPRE	IL2003	KS1999	NE1993	MN1992
ILPRE	-	0.0236	0.0275	0.0242	0.0315
IL2003	0.00108	-	0.0196	0.0198	0.0284
KS1999	0.00115	0.00026	-	0.0059	0.0152
NE1993	0.00114	0.00027	0.00019	-	0.0094
MN1992	0.00122	0.00032	0.00023	0.00019	-

translocations, there was a marked reduction in differentiation between the Illinois population (IL2003) and the source populations, suggesting introgression of genomic variation. Patterns of differentiation between IL2003 and the source populations were consistent with the relative magnitude of translocations from each source population. For instance, the source population that provided the fewest number of translocated individuals (MN1992) exhibited the highest differentiation with IL2003. Moreover, levels of differentiation between the Illinois pre- and post-translocation populations were comparable with those between ILPRE and the source populations. For example, the Φ_{ST} between ILPRE and NE1993 was 0.0242, while the ILPRE-IL2003 comparison had a value of 0.0236. The relatively high level of differentiation between ILPRE and IL2003 further indicates introgression of translocated individuals. In addition, the degree of differentiation among source populations corresponds with geographic distance and/or habitat connectivity. The populations nearest one another, KS1999 and NE1993 exhibited the lowest differentiation ($\Phi_{ST} = 0.0059$) while those farthest apart, KS1999 and MN1992, showed the highest differentiation ($\Phi_{ST} = 0.0152$). We found qualitatively similar patterns of differentiation when controlling for linked SNPs and differences in both the number of loci per population and the number of individuals per population. As no more than 2.7% of SNPs per population significantly deviated from Hardy–Weinberg equilibrium (HWE), SNPs were not filtered by HWE p-values when calculating differentiation estimates.

Population structure

To assess relative genetic structure of the source and recipient populations preceding translocations, principal component analysis (PCA) was performed on non-linked SNPs genotyped in all source populations and ILPRE (Fig. 2a). We found that most populations showed distinct clustering along both the first and second principal components (PCs), which explained 2.6% and 2.3% of the total observed variation, respectively (illustrated by their corresponding density plots). With the exception of KS1999 and NE1993, all population clusters were significantly different within the PC space, as demonstrated by their non-overlapping 99% confidence interval ellipses. Source populations displayed clustering patterns consistent with levels of pairwise differentiation, with geographically distant populations (e.g. KS1999 and MN1992) clustering farther in the PC space. The Illinois pre-translocation population (ILPRE) shows the most distinctive genetic variation, clustering farthest away from the source populations along both PC axes.

PCA was performed a second time including the Illinois population sampled 7 years after the completion of translocations (IL2003) to assess changes in genomic variation

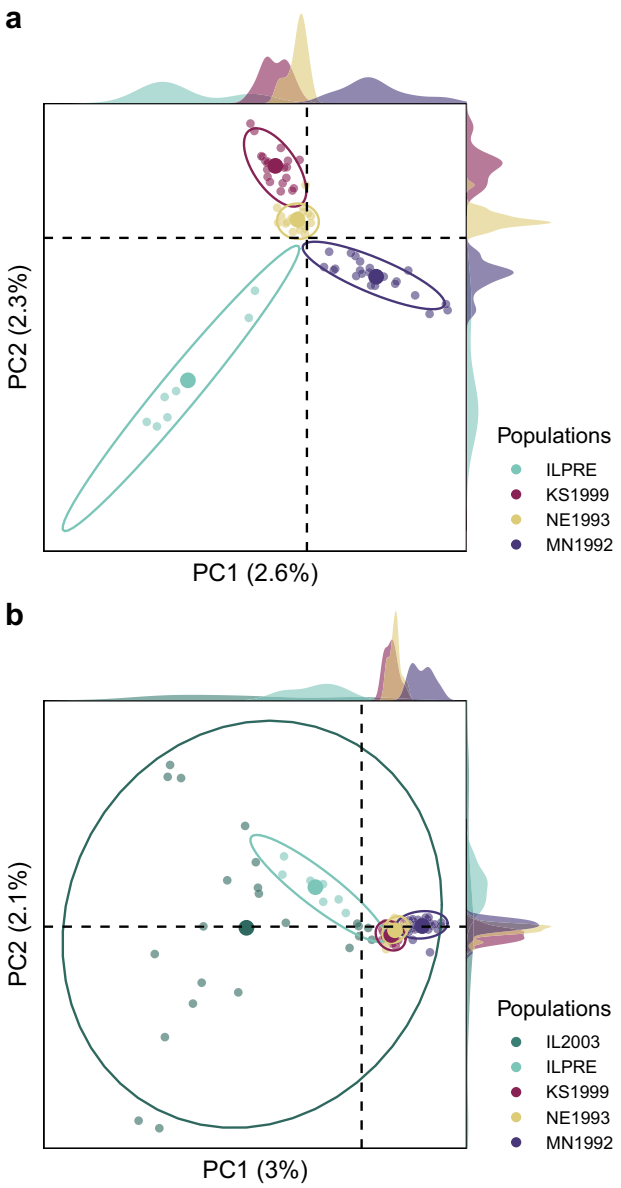

Fig. 2 Principal component analyses with density plots of PC1 and PC2 for (**a**) ILPRE and source populations and (**b**) for all populations. Horizontal density plots correspond to PC1 while vertical density plots correspond to PC2. Included are 99% confidence intervals (ellipsis) centered around the population mean value. The percent variation explained by each PC is shown in parentheses. Dotted lines represent axes with origin of (0,0)

(Fig. 2b). Following the translocations, samples from IL2003 were widely dispersed along both PC1 and PC2. The IL2003 population completely overlapped ILPRE and a portion of KS1999 and NE1993 along PC1 and comprise all PC space occupied by the other populations along PC2. Hence, the IL2003 99% confidence interval encompasses the PC space of all other populations, suggesting that translocations resulted in a population harboring genetic variation from the ancestral pre-translocated Illinois population (ILPRE) as

well as the three source populations used for translocations (KS1999, NE1993, and MN1992).

Population structure was further delineated by more quantifiable measures using Bayesian assignment of genetic clusters, based on SNP frequencies, utilizing the program Structure (Pritchard et al. 2000). All estimators utilized (i.e. MedMeaK, MaxMeaK, MedMedK, and MaxMedK) identified the most probable number of genetic clusters as five ($K=5$; Fig. 3). Source populations were separated into three distinct genetic clusters with evidence of gene flow or recent shared ancestry between NE1993 and KS1999 as well as between NE1993 and MN1992. ILPRE parsed into a major (cluster 1) and minor (cluster 2) genetic cluster, which exhibited limited and no shared assignment with the source populations, respectively.

The Illinois population following the translocations (IL2003) was largely a mix of the genetic clusters dominated by or unique to ILPRE (mean assignment = 0.127 and 0.616, respectively) as well as the genetic cluster representative of KS1999 (mean assignment = 0.234). The mean assignment of genetic clusters within IL2003 is highly congruent with the relative magnitude of translocations from each source population—the vast majority of translocated individuals came from Kansas (196 individuals), which showed the highest mean assignment, followed by Nebraska (50 individuals translocated), the next highest mean assignment (0.021), and finally Minnesota (27 individuals translocated) with the lowest mean assignment (0.003).

Private alleles

Population-level counts of private alleles revealed that every population (ILPRE, KS1999, NE1993, and MN1992) possessed a significant number of private alleles (Table 2). MN1992 possessed the largest number of private alleles (261), followed by KS1999 and NE1993 (81 and 80, respectively), with ILPRE containing the fewest number of private alleles (18), consistent with the small sample size available. When normalized by population sample size, ILPRE, KS1999, and NE1993 had similar numbers of private alleles per individual (2.57, 3.86, and 3.2 respectively) while MN1992 had, proportionally, a much larger number of private alleles per individual (10.44). The majority (55.6%)

Table 2 Population-level private allele summary

Population	# P.A	# P.A. in IL2003	% P.A. in IL2003
ILPRE	18	10	55.6%
KS1999	81	38	46.9%
NE1993	80	38	47.5%
MN1992	261	78	29.9%

Includes population from which private alleles originated (Population), raw number of private alleles detected in each population of origin (# P.A.), total number of private alleles detected in the IL2003 post-translocation population (# P.A. in IL2003), and private alleles detected in IL2003 as a percent of the total number of private alleles detected in the respective population of origin (% P.A. in IL2003)

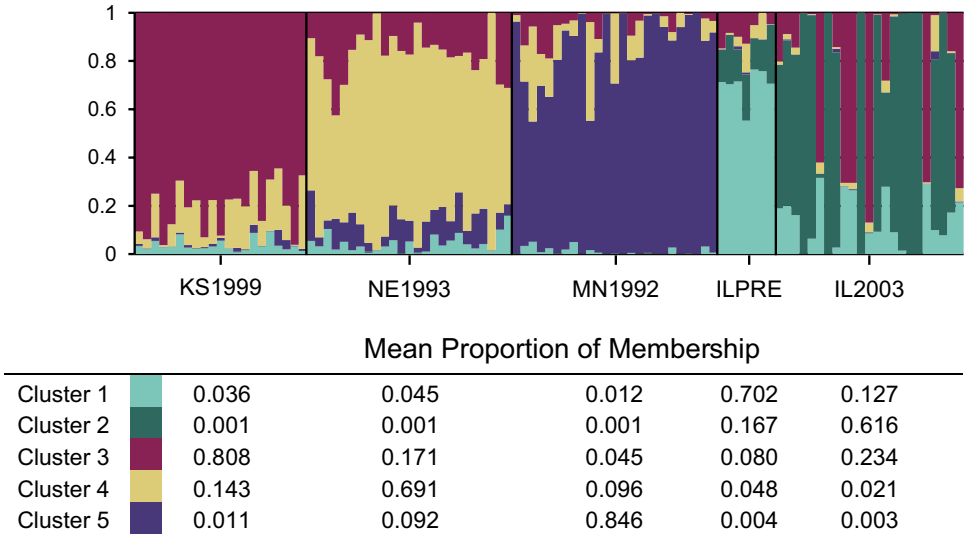

Fig. 3 Estimated population structure for source populations (KS1999, NE1993, and MN1992) and the Illinois population prior to (ILPRE) and following (IL2003) translocations as determined by Structure given K = 5. The given consensus plot was constructed using CLUMPAK for the major mode of clustering found across 6 out of 10 runs of K = 5. Individuals are represented by vertical bars indicating their estimated membership to given genetic clusters (cluster 1–5). Vertical black lines separate sampling locations. Average population cluster assignments are also indicated (below bar plot) with each column of values showing the overall proportions of cluster assignment for each corresponding population in the Structure plot above

of Illinois pre-translocation (ILPRE) private alleles persisted in the IL2003 population. IL2003 also possessed private alleles from every source population (KS1999, NE1993, and MN1992). The relative proportions of private alleles originating from source populations detected in IL2003 correlated with the relative magnitude of translocations from each state. In particular, the state that contributed the fewest individuals (MN1992) exhibited the lowest percentage of private alleles detected in Illinois post-translocation (29.9%).

Individual-level counts of private alleles illustrate heterogeneity in relative proportions of ancestry among IL2003 individuals (Fig. 4). All IL2003 individuals possessed private alleles from each source population. However, the relative proportions of private alleles from each source population exhibited high variation among individuals (KS1999 ranged 0.065–0.438, NE1993 ranged 0.092–0.563, MN1992 ranged 0.064–0.340). Our results also show that most individuals (20/23) sampled from IL2003 possessed private alleles that were present before the translocations (i.e. ILPRE private alleles). Among these, five individuals showed greater than 50% inferred ancestry to the Illinois pre-translocated population. Conversely, three individuals lacked private alleles originating from the Illinois pre-translocation population all together.

Discussion

Although Illinois greater prairie-chicken have been hailed as a conservation icon since the late 1990s due to measured increases in fitness immediately following translocations, detailed impacts on genomic diversity had not been successfully captured until now. By employing thousands of genome-wide markers produced via RADseq, we have delineated patterns of genomic diversity, population structure, and introgression among the source, pre-, and post-translocation populations involved in this long-term study. Through comprehensive and fine-scale tracking of genomic variation among source and recipient populations, we have documented that species translocations can result in successful genetic restoration of endangered populations through alleviation of inbreeding, restoration of evolutionary potential, and maintenance of local variation.

Prior to the initiation of translocations, we found that the Illinois population was genetically distinct from the source populations, likely due to significant genetic drift and inbreeding resulting from complete isolation from all other prairie-chicken populations since the early twentieth century. The analysis of genome-wide loci revealed that translocations resulted in the recovery of genomic diversity within the previously highly inbred and genetically depauperate Illinois population to levels akin to those observed in the source populations. This increase in variation can be directly attributed to introgression from all source populations. Following the translocations, patterns of pairwise population differentiation exhibited a reduction in genetic disparity between the Illinois population and each source population. The PCA, Structure analysis, and private allele analyses all consistently indicated that the previously genetically distinct Illinois population gained significant variation from the individual source populations while maintaining variation unique to Illinois. The relative degree of introgression of source-specific variation into Illinois was consistent with the relative degree of translocation from each source population, as demonstrated by the Structure and private allele results, suggesting equal opportunity for genetic contribution among translocated individuals.

Genome-wide analysis of SNP datasets produced via reduced-representation sequencing techniques like RADseq allows precise definition and assessment of translocation success by measuring large and fine-scale variation of source and recipient populations prior to and following population management. Most noteworthy here is that genomic data provided the resolution needed for tracking

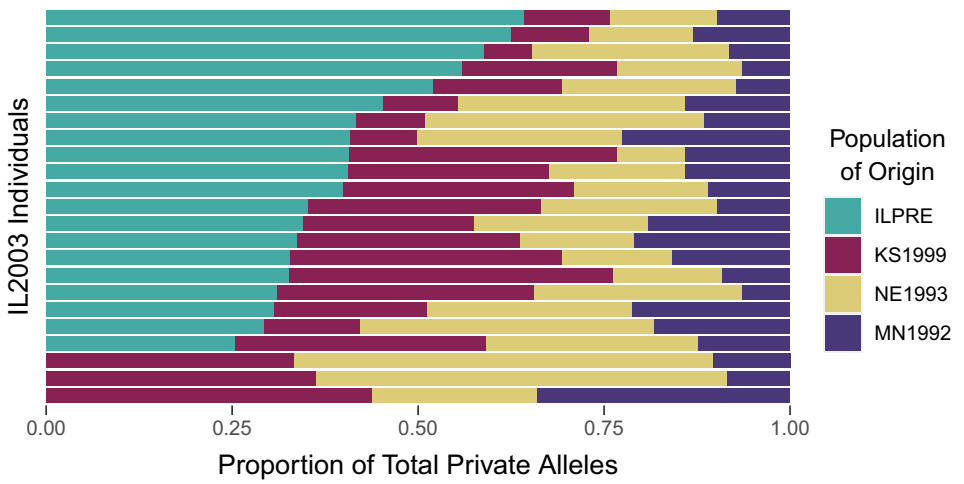

Fig. 4 Inferred ancestry of individuals sampled from the Illinois post-translocation population (IL2003). Ancestry for each IL2003 individual is represented by the proportion of private alleles from each population (ILPRE, KS1999, NE1993, MN1992) normalized by the respective total possible number of private alleles from each population and total number of private alleles detected within each individual

levels of introgression from each source population through the analysis of private alleles, and hence, the success of individual translocation events, a novel approach to conservation management. The population genomic analysis of the greater prairie-chicken is employed here as a case study to demonstrate that the success of translocations as a conservation management tool can be assessed for all three criteria defined by genetic restoration: (1) the alleviation of inbreeding for short-term viability, (2) the restoration of evolutionary potential for long-term survival, and (3) the maintenance of local variation to prevent genomic swamping.

Alleviation of inbreeding for short-term viability

When translocation success is measured using genetic data, success is most often characterized as an increase in genetic diversity through introduction of distantly related individuals, leading to alleviation of inbreeding and its detrimental effects on fitness, a process often referred to as genetic rescue (Hedrick 2005). Results from our RADseq dataset of 356,778 SNPs revealed a clear and consistent signal that translocations effectively alleviated high levels of inbreeding in the recipient population through successful introgression individuals from genetically differentiated populations, restoring heterozygosity to levels consistent with those of non-bottlenecked source populations. While previous studies attempted to infer levels of inbreeding through measures of genetic diversity prior to (Bouzat et al. 1998a, b; Westemeier et al. 1998) and following translocations (Bouzat et al. 2009; Mussmann et al. 2017), the limited number of loci assessed restricted detection of significant effects on the post-translocation population. Our study exemplifies that large SNP datasets offer a precise tool to evaluate the genetic effects of translocations on key parameters (e.g. Ho, He, and F_{is}) directly associated with inbreeding depression. The broad-scale effects of translocations on measures of heterozygosity have been explored across a variety of species. However, while they have observed effects on measures of heterozygosity comparable to our findings, other studies have either employed small-scale genetic techniques (Johnson et al. 2010; Lemer and Planes 2012; Bateson et al. 2014; Zimmerman et al. 2019) or assessed changes in genomic variation indirectly due to lack of pre-translocation sampling (Dresser et al. 2017).

From a conservation perspective, the precision afforded by large SNP datasets in measuring overall levels of genomic diversity provides the basis to define, a priori, a specific standard of success for genetic rescue. Here, we propose the average estimate of genetic diversity from all source populations as an appropriate minimum target for success for this and future translocation programs. In this case, source populations maintained relatively stable population numbers and showed no clear evidence of inbreeding depression (Svedarsky et al. 2000; McNew 2010; Matthews et al. 2013), providing reference points for "healthy" levels of genome-wide diversity. This explicit goal allowed us to conclude that, in the case of the Illinois greater prairie-chicken, translocations were successful in alleviating inbreeding. However, recommending this goal for translocations exemplifies the necessity for genetic sampling of the recipient population prior to the implementation of any translocation plan, a management strategy that is not always followed.

Restoration of evolutionary potential for long-term survival

The process of genetic restoration seeks to broaden the definition of success beyond genetic rescue by incorporating the restoration of evolutionary potential of the recipient population(s). Whereas inbreeding results in loss of individual-level diversity through increased homozygosity, severe population contractions also result in the loss of population-level diversity through allele fixation via genetic drift and restricted gene flow. Significant loss of genomic diversity through allele fixation over time can impede a population's ability to respond to fluctuating environmental pressures, restricting its evolutionary potential (Frankham 1995; Haig and Avise 1996; Frankham et al. 1999). However, evolutionary potential may be restored, or at least improved, through re-introduction of lost alleles and/or introgression of novel alleles through translocations from non-bottlenecked populations.

In the example of the Illinois greater prairie-chicken, we identified a large number of differentiating SNPs among the recipient and source populations, allowing the quantification of genetic differentiation, population structure, and levels of introgression into the target population. Our results indicated that translocations from genetically distinct populations successfully increased allelic diversity and shifted genomic variation of the genetically depauperate Illinois population to one encompassing variation from all three source populations. At the individual level, every sample from IL2003 showed some degree of ancestry to each of the source populations, further demonstrating the effectiveness of translocations in increasing the gene pool of the Illinois population. The high genomic heterogeneity instilled in Illinois through successful introgression from each translocation event likely offers the population vastly improved evolutionary potential, increasing its probability for long-term viability. However, we recognize that samples taken from the post-translocation population are nearly two decades old, and therefore characterize the population shortly after the completion of translocations. Other studies that have assessed population genetic diversity of grouse species a decade or more following translocations have found that variation either returned to or dropped below pre-translocation levels as a result of

continued genetic drift (Bateson et al. 2014; Zimmerman et al. 2019). While available habitat has increased through restoration efforts (Bouzat et al. 2009), counts in both Illinois greater prairie-chicken populations have once again declined to near pre-translocation levels, prompting a second round of translocations in 2014 (S. Simpson, unpublished data). Without maintaining substantially larger population sizes following translocations through further increased habitat and population connectivity, especially in a species with reduced effective population size due to highly skewed breeding sex ratios, genetic drift will likely erode the beneficial effects of translocations.

Maintenance of local variation: preventing genomic swamping

While the introduction of genetic variation is important for decreasing rates of inbreeding and restoring genetic diversity for long-term viability, equally important is the maintenance of local variation for retaining population-specific adaptation. A major concern in performing translocations is the possibility that local adaptative variation may be either altered significantly (e.g., by disruption of co-adaptive gene complexes; Shields 1982; Templeton 1986) or completely eliminated through genetic swamping by translocated individuals (Templeton 1986; Slatkin 1987).

Despite the translocation of a substantial number of birds, our results signify that the Illinois population retained a significant amount of local variation 7 years following the completion of translocations. Along the first principal component, the Illinois post-translocation population most overlaps with the Illinois pre-translocation population, suggesting a higher degree of shared ancestry than with the source populations. Characterization of genetic variation among populations through Structure showed that the post-translocation population retained about 74% of variation associated with Illinois as determined by Bayesian estimates of membership to each cluster (Fig. 3, clusters 1 & 2). The analysis of private alleles also indicated maintenance of Illinois pre-translocation variation, as the majority of unique genetic variants were detected post-translocation across nearly all individuals sampled. Our results revealed, therefore, that translocations did not result in massive genomic swamping, as significant levels of local genomic diversity were retained. Previous studies attempting to measure post-translocation ancestry have relied largely on inferred genetic clustering methods like Structure rather than direct tracking of private alleles (Lemer and Planes 2012; Miller et al. 2012). However, our analyses demonstrate that, alongside established tools like PCA and Structure, detection of private alleles across populations provides a powerful approach for directly detecting levels of introgression and retention of local variation in populations of conservation concern.

The maintenance of local variation alone does not fully encapsulate the third major principle of genetic restoration, which emphasizes the preservation of local *adaptive* variation. While likely as vital as increasing neutral variation, the retention of adaptive differentiation among source and recipient populations is generally not a primary concern when developing translocation programs. However, neglecting potential adaptive differences among populations could result in the disruption of local adaptation, leading to outbreeding depression in the resultant admixed population, consequently undermining management efforts. Genomic techniques allow for targeted or incidental sequencing of loci directly associated with ecologically relevant traits or traits associated with fitness. Population-level studies of genome-wide markers give investigators the ability to identify specific variation under selection (e.g. QTLs or genes associated with fitness; Hohenlohe et al. 2010; Andrews et al. 2016), allowing investigation of the retention of local adaptive variation. Outbreeding depression could potentially be avoided in admixed populations by measuring adaptive differentiation among potential source and recipient populations prior to the initiation of translocations. By identifying potential source populations with minimal adaptive differentiation in conjunction with high neutral variation, a priori, translocations may well see increased long-term success. We recognize that not all projects possess the species-specific genomic resources or analytical expertise to effectively employ these techniques. However, the number of high-quality annotated reference genomes is continually expanding (Lewin et al. 2018) and wide-spread use of these techniques in universities and other institutions across the world offer extensive opportunities for collaboration.

We have employed the greater prairie-chicken as a case study to demonstrate the power of population genomics to define and evaluate the success of species translocations. To our knowledge, this is the first instance of applying a large RADseq dataset to precisely track genomic variation before and after translocations. Our results have proven that population genomic approaches facilitate evaluation of the genomic components of genetic restoration: (1) the alleviation of inbreeding for short-term viability, (2) the restoration of evolutionary potential for long-term survival, and (3) the maintenance of local variation for prevention of genetic swamping. Ultimately, we understand that long-term translocation success is contingent on addressing the initial cause of population endangerment, which for most species is habitat loss and fragmentation (Soulé 1986). We also acknowledge that tracking long-term translocation success requires follow-up sampling to detect potential negating forces such as continued genetic drift and outbreeding depression. Furthermore, we recognize that, although highly informative, measuring the genome-wide impacts of translocations only provide part of the picture genetic restoration

seeks to capture. In most cases, conclusions drawn about population viability are limited by a lack of ecological data directly related to estimates of lifetime reproductive success and their effects on extirpation. Nonetheless, understanding the genomic impacts of species translocations offers a broad picture of the genomic health of populations, affording managers the opportunity to tailor and improve future management decisions at a scale not previously seen. We believe that the current state of ambiguous goals and lack of long-term monitoring seen in translocations hinders managers' ability to effectively conserve populations on the verge of extinction. Genomic data derived from genomic techniques like RADseq offer those seeking to conserve wild populations affordable and widely available tools to understand and improve the efficacy of conservation management.

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Data availability The raw sequencing data used for this work will be submitted to the Sequence Read Archive upon acceptance.

Code availability Custom scripts employed to analyze data are available at https://github.com/slcapel/snp-population-level-private-allele-tracker and https://github.com/slcapel/snp-individual-private-allele-distributions

Declarations

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