The Genetic and Evolutionary Basis of Spring Run-timing in Chinook: The Current State of the Science

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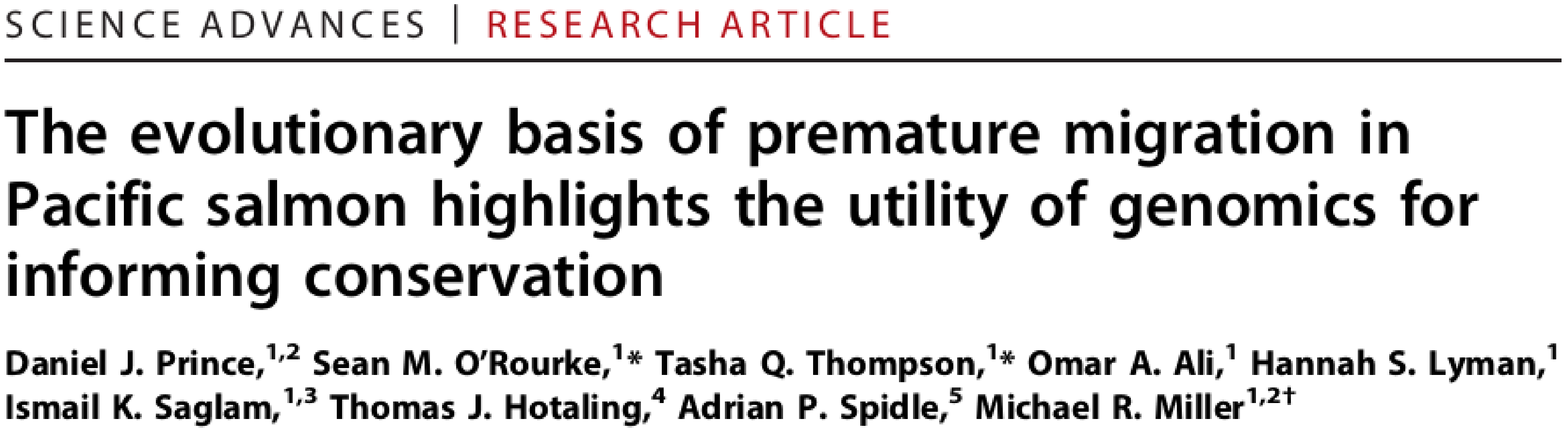
UCDAVIS
DEPARTMENT OF ANIMAL SCIENCE

My lab has focused on studying the genetics and evolution of spring Chinook for almost 10 years now.



SCIENCE ADVANCES | RESEARCH ARTICLE

The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation

Daniel J. Prince,[1,2] Sean M. O'Rourke,[1]* Tasha Q. Thompson,[1]* Omar A. Ali,[1] Hannah S. Lyman,[1] Ismail K. Saglam,[1,3] Thomas J. Hotaling,[4] Adrian P. Spidle,[5] Michael R. Miller[1,2]†

Publicly available since June 2016

Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations

Tasha Q. Thompson[a,b,1], M. Renee Bellinger[c,2], Sean M. O'Rourke[a,b,2], Daniel J. Prince[a,b,2], Alexander E. Stevenson[d], Antonia T. Rodrigues[e], Matthew R. Sloat[f], Camilla F. Speller[g,h], Dongya Y. Yang[e], Virginia L. Butler[i], Michael A. Banks[c], and Michael R. Miller[a,b,1]

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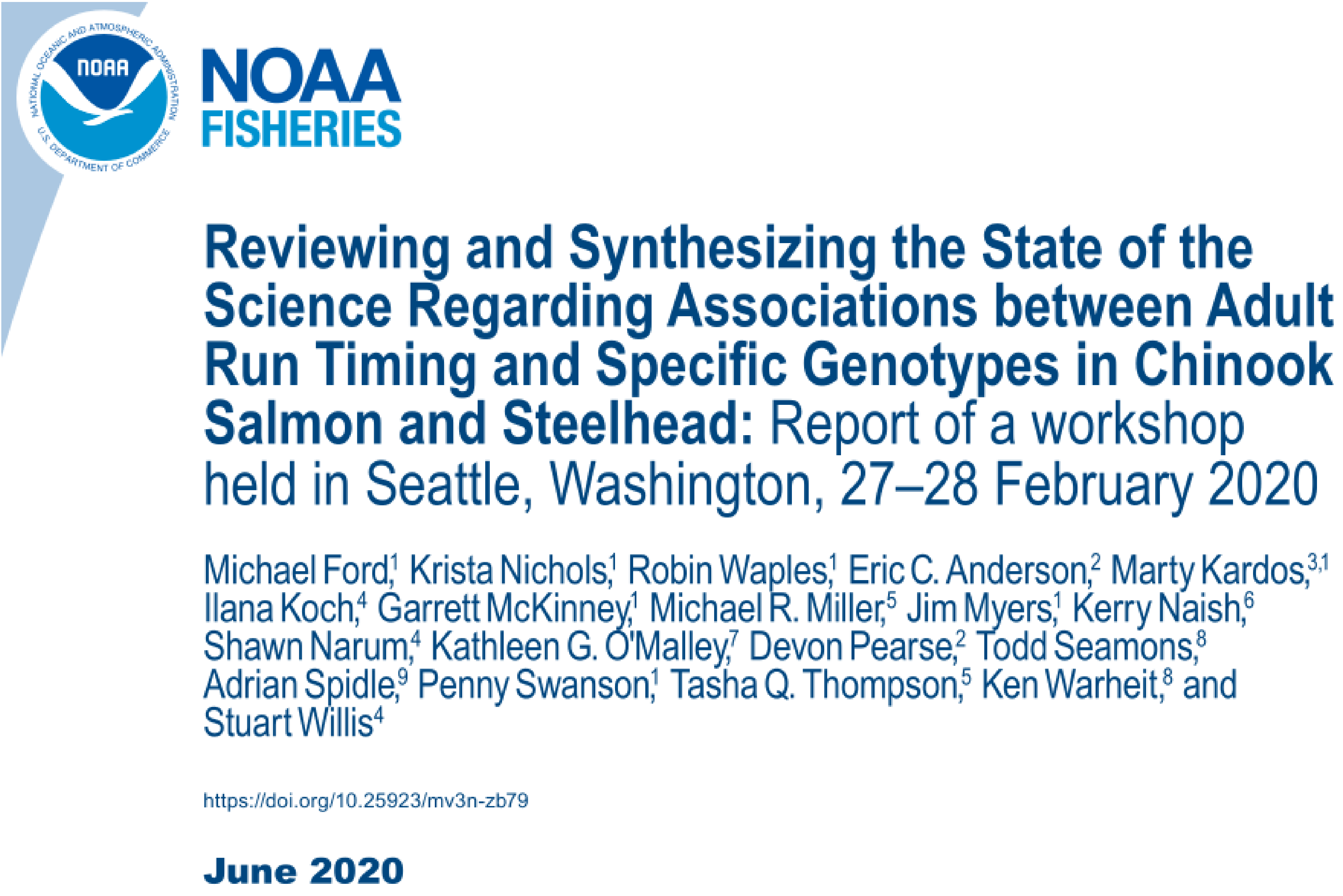
A recently published report reviews and synthesizes the state of the science on spring Chinook genetics.



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Reviewing and Synthesizing the State of the Science Regarding Associations between Adult Run Timing and Specific Genotypes in Chinook Salmon and Steelhead: Report of a workshop held in Seattle, Washington, 27–28 February 2020

Michael Ford,[1] Krista Nichols,[1] Robin Waples,[1] Eric C. Anderson,[2] Marty Kardos,[3,1] Ilana Koch,[4] Garrett McKinney,[1] Michael R. Miller,[5] Jim Myers,[1] Kerry Naish,[6] Shawn Narum,[4] Kathleen G. O'Malley,[7] Devon Pearse,[2] Todd Seamons,[8] Adrian Spidle,[9] Penny Swanson,[1] Tasha Q. Thompson,[5] Ken Warheit,[8] and Stuart Willis[4]

https://doi.org/10.25923/mv3n-zb79

June 2020

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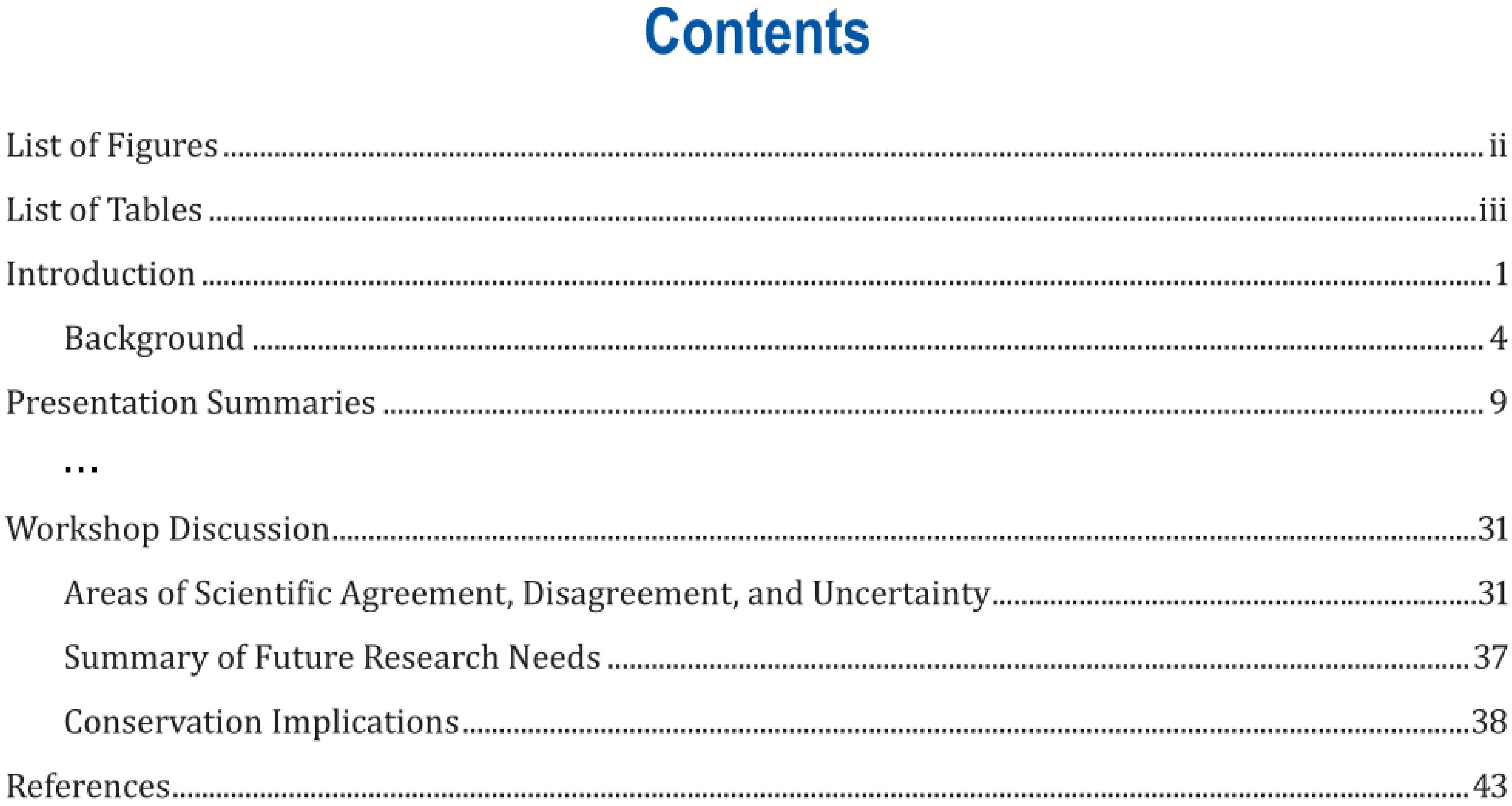

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Ford *et al.* 2020

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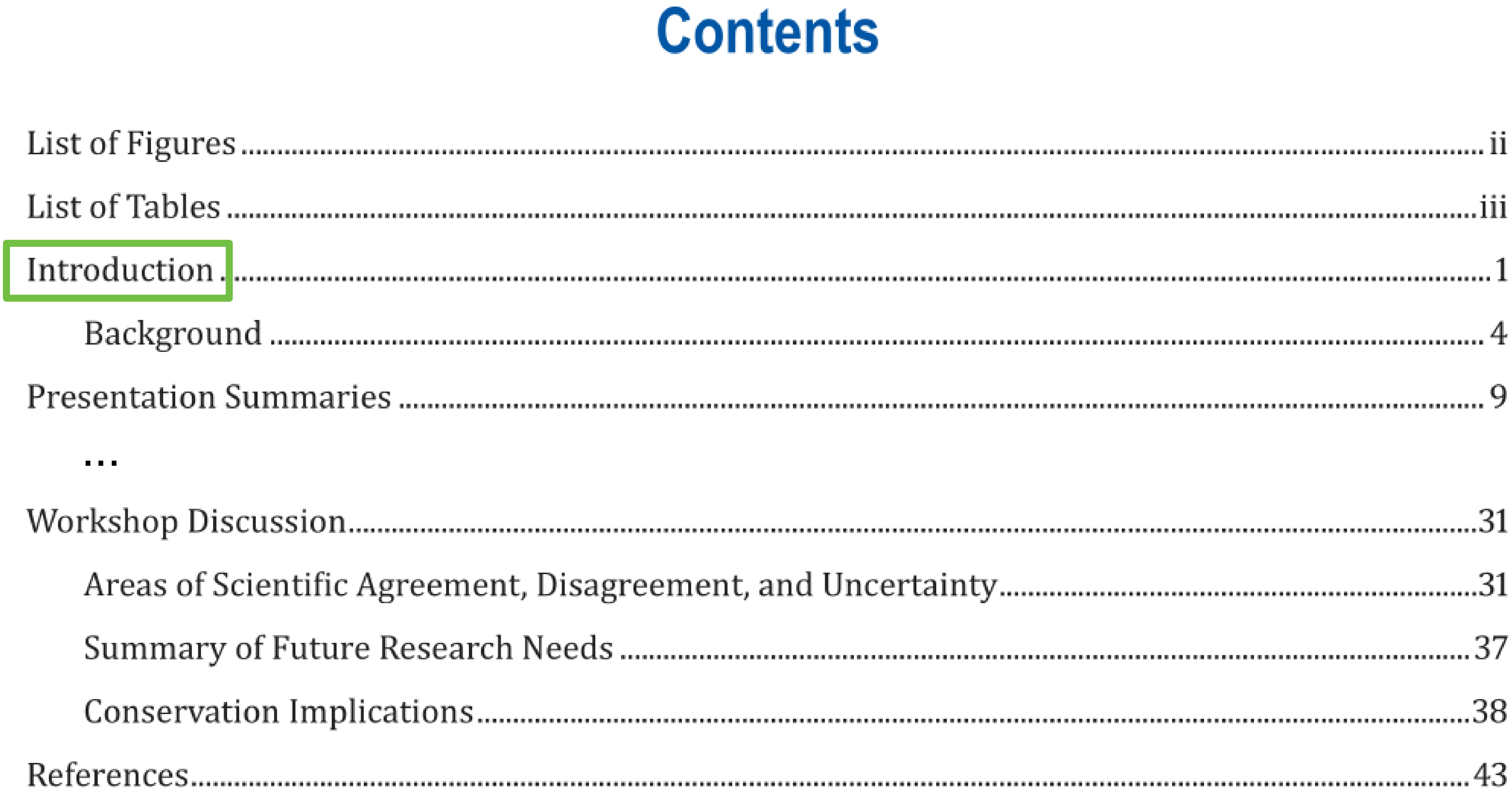

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Ford *et al.* 2020

Introduction

“The goal of the workshop was to characterize the current state of the science regarding the nature of the associations between genetic variation and run timing in Chinook salmon and steelhead… It is important to clarify that, although we found it useful to identify areas of scientific agreement where they exist, in general we made no attempt to find consensus among the participants; instead, this report attempts to reflect the full range of views of participants on the issues that were discussed.”

Ford *et al.* 2020

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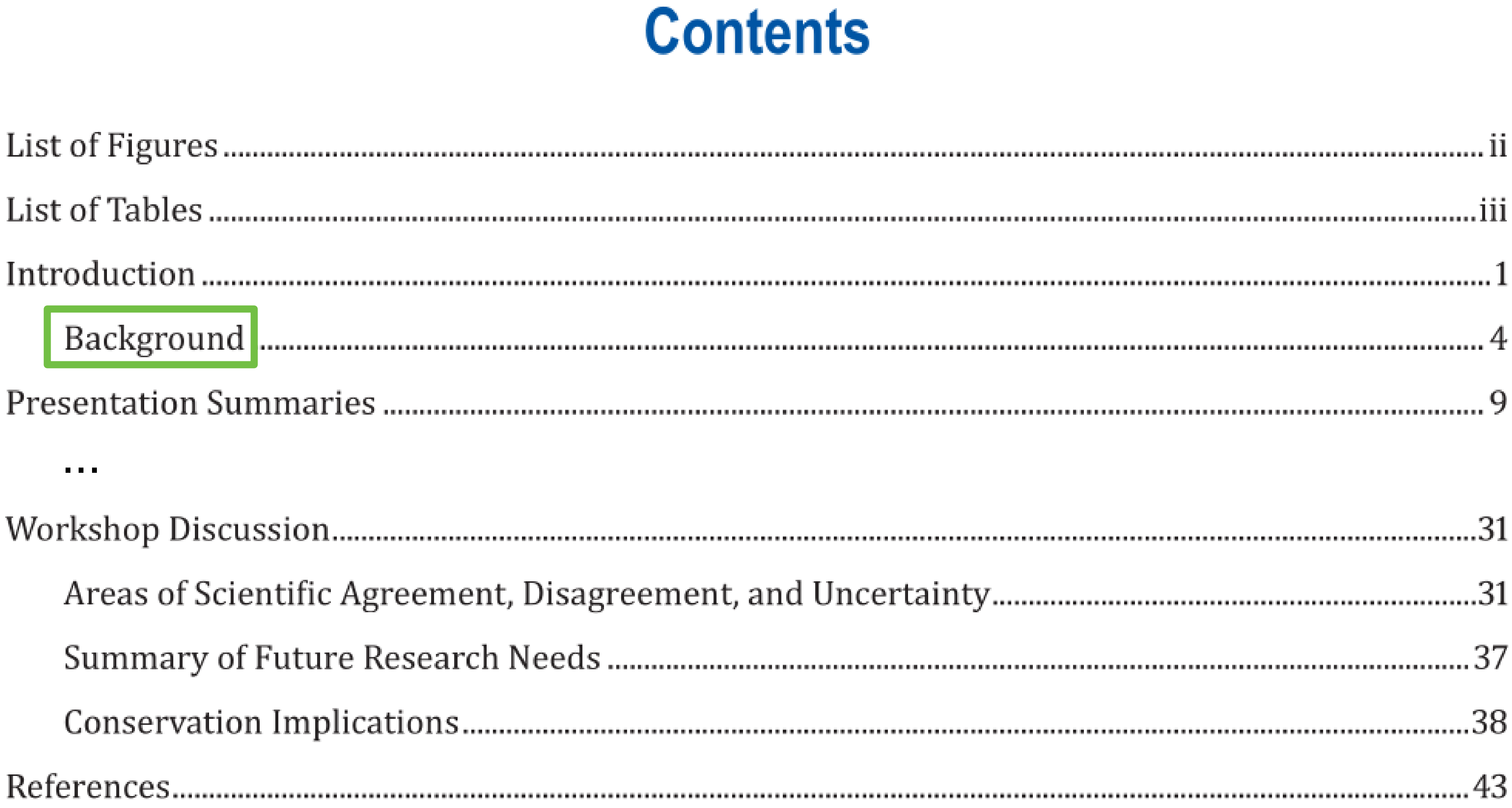

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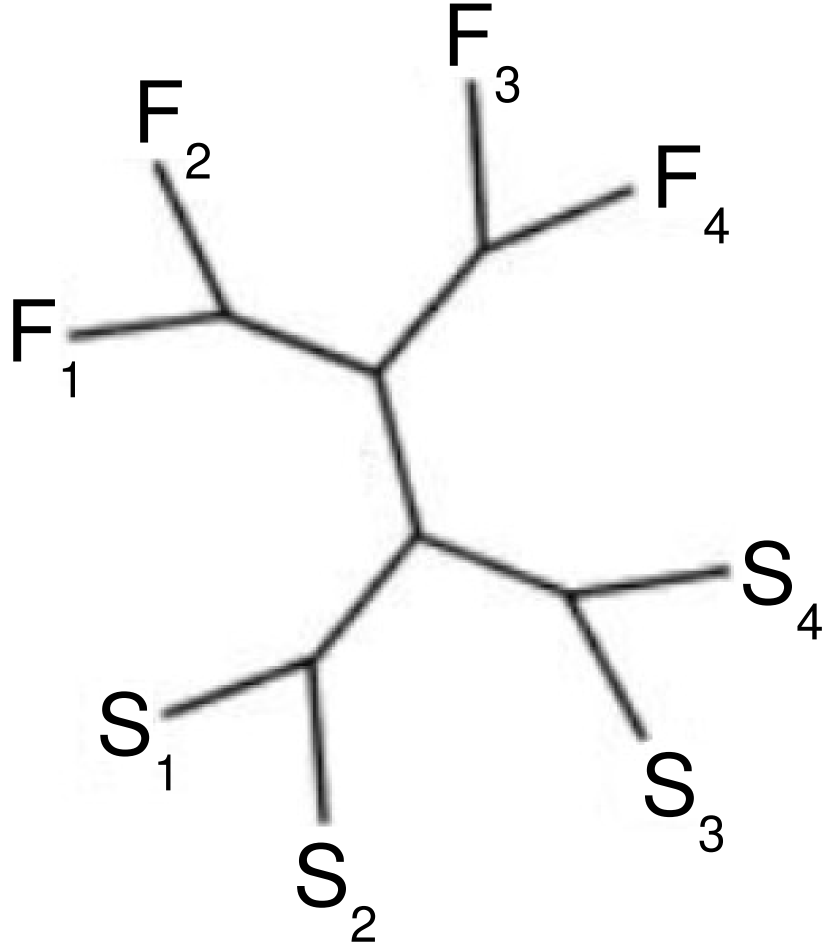
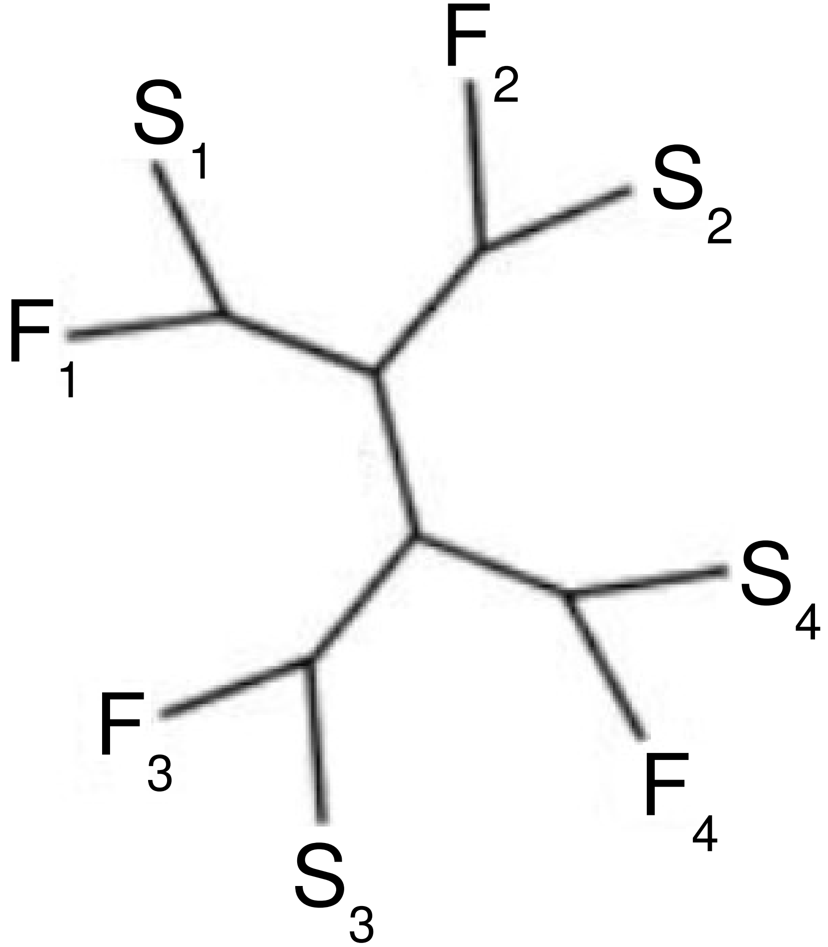
Ford *et al.* 2020

Previous studies found the genetic relationship among populations relates to geography as opposed to migration type (i.e., spring-run or fall-run).





e.g., Waples *et al.* 2004

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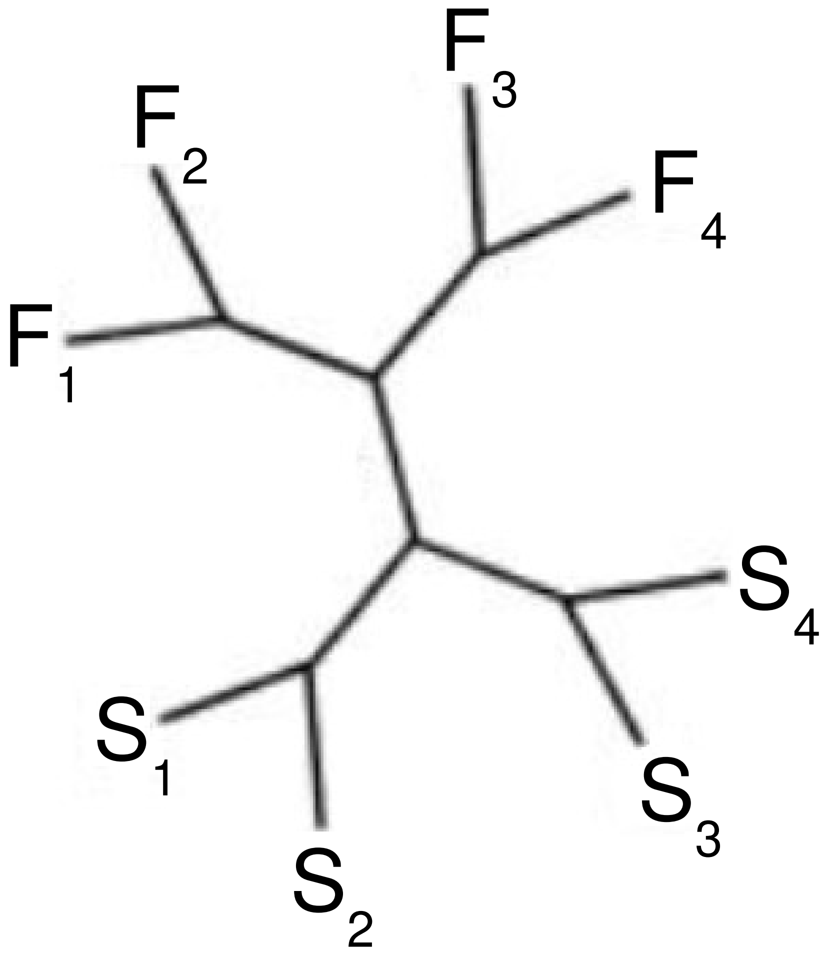

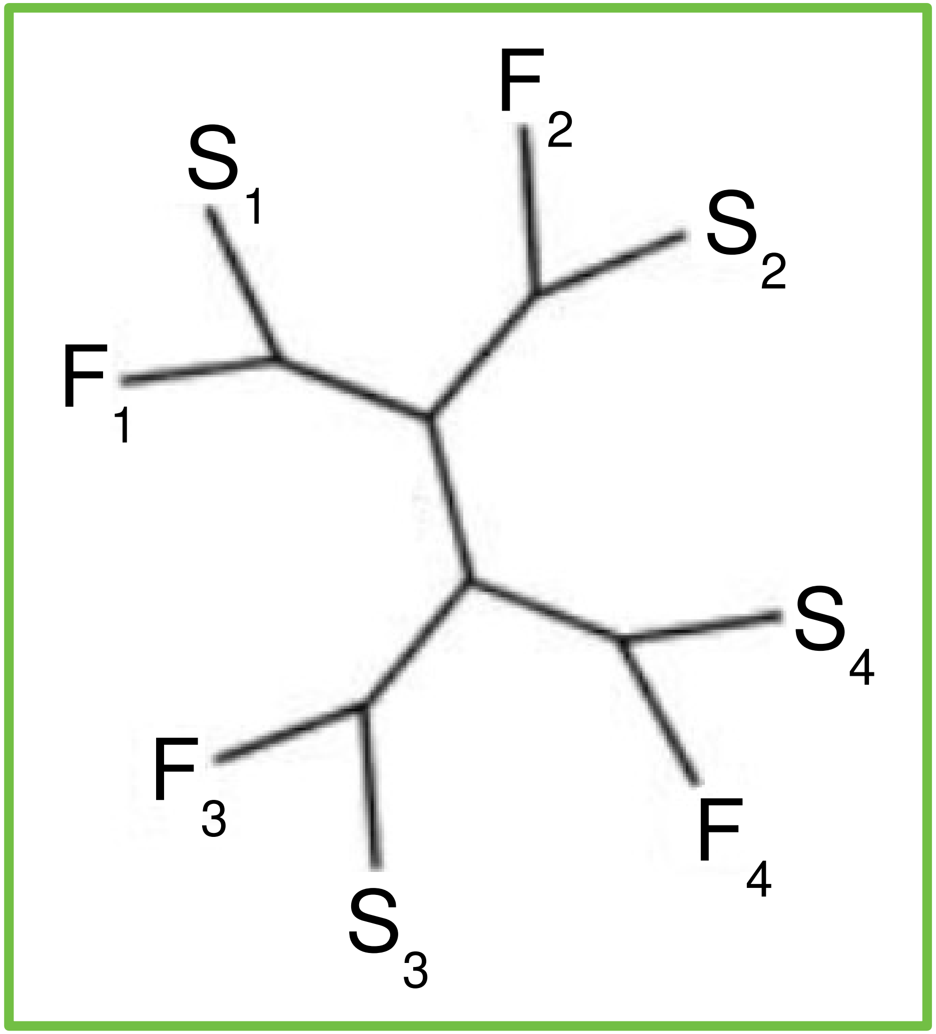

e.g., Waples *et al.* 2004

These results were interpreted to suggest that spring Chinook evolved independently in different rivers.

“These results suggest that the different times of return may have evolved independently in the different river systems.”

Thorgaard 1983

“These results indicate that run-timing diversity has developed independently by a process of parallel evolution… [Run-timing diversity] appear[s] to be evolutionarily replaceable, perhaps over time frames of a century or so.”

Waples *et al.* 2004

Background

“Based on these results, it was concluded that adult run-timing differences had evolved independently many times within both Chinook salmon and steelhead... Furthermore, it was thought that the early-migration phenotype could evolve from mature migrators on relatively short timescales (perhaps around 100 years; Waples et al. 2004). Therefore, in defining ESUs of coastal and lower Columbia River populations in both species, it was concluded that adult run-timing differences reflected diversity within ESUs.”

Ford *et al.* 2020

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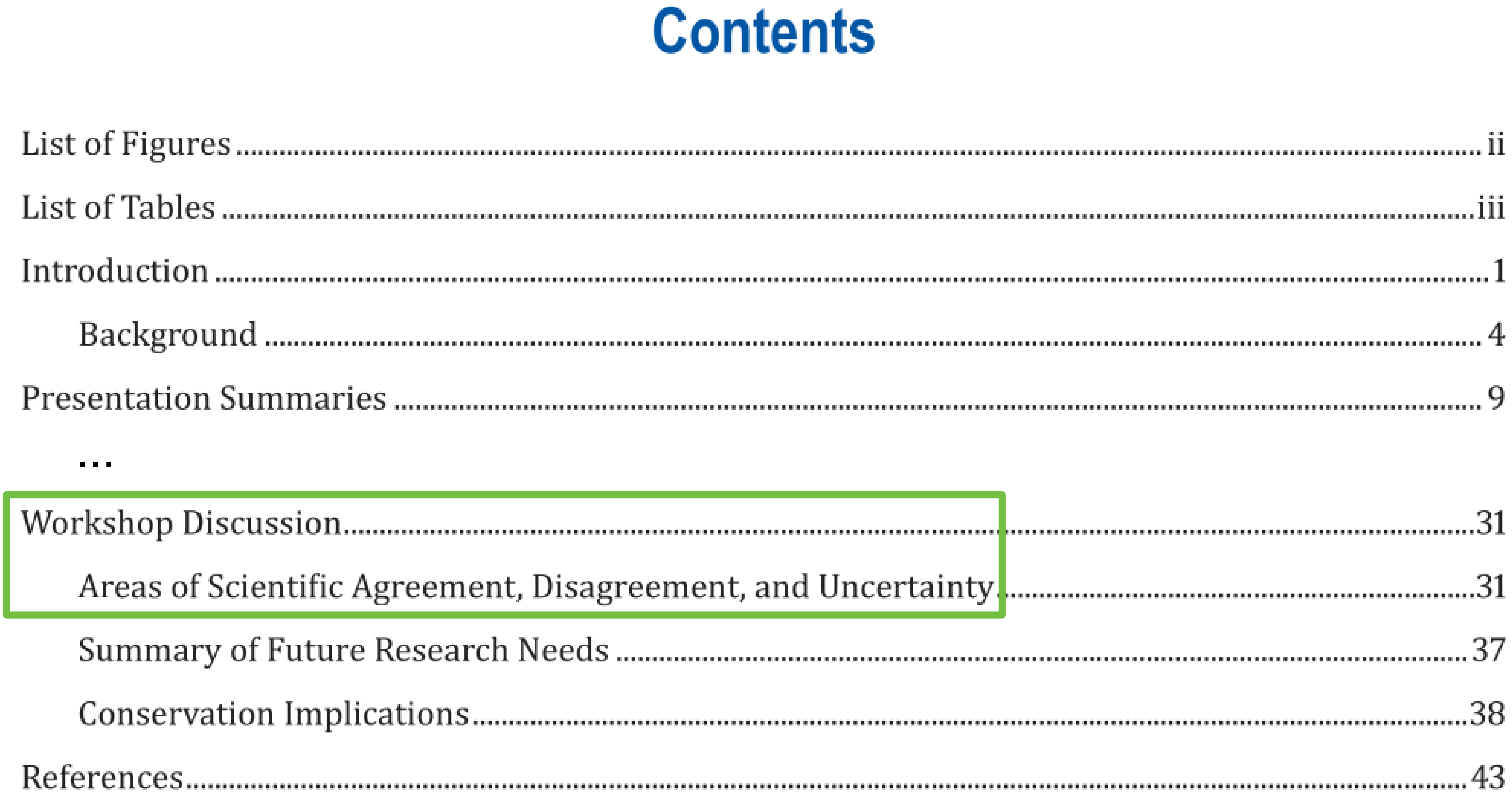

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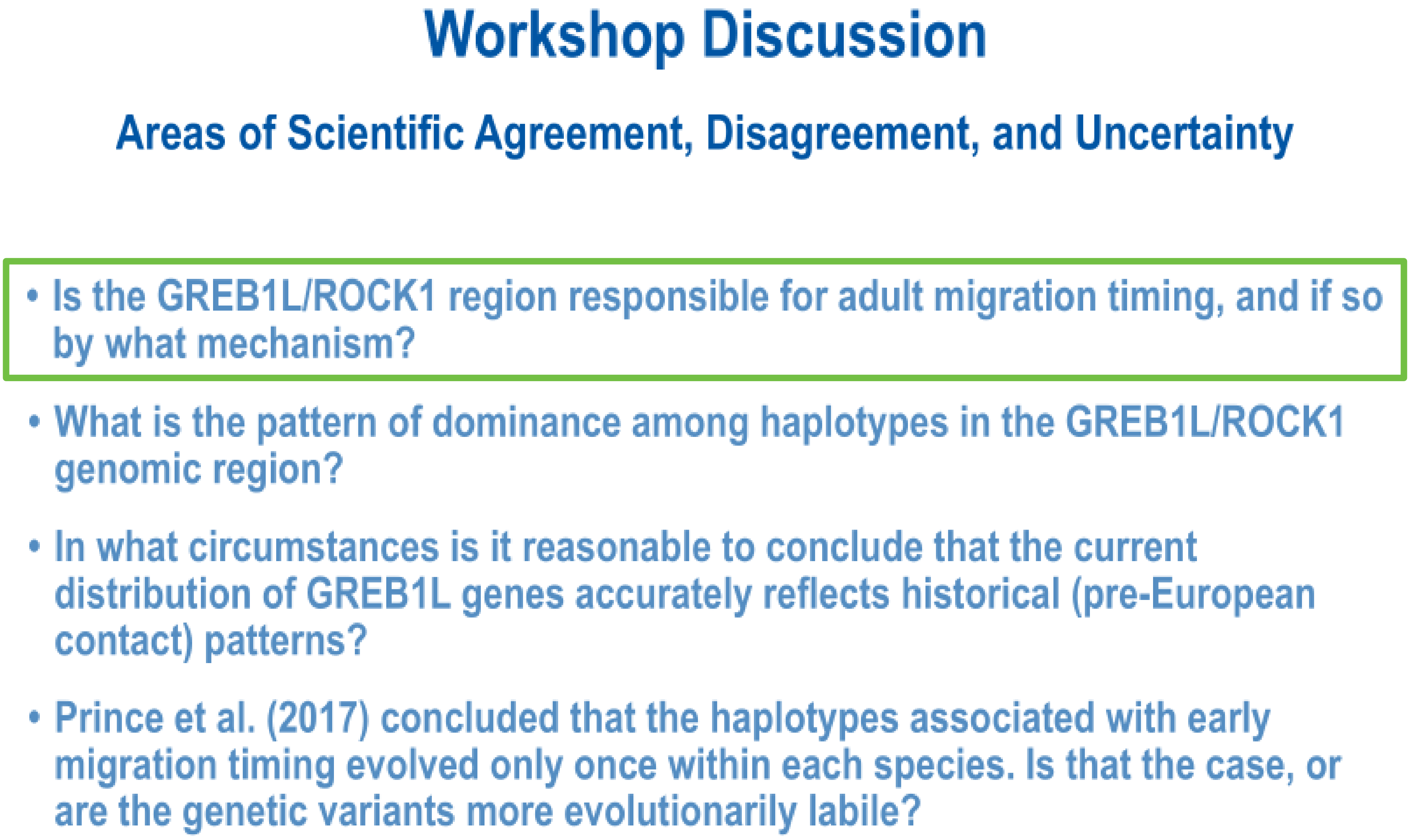
Workshop Discussion

Areas of Scientific Agreement, Disagreement, and Uncertainty

- Is the GREB1L/ROCK1 region responsible for adult migration timing, and if so by what mechanism?
- What is the pattern of dominance among haplotypes in the GREB1L/ROCK1 genomic region?
- In what circumstances is it reasonable to conclude that the current distribution of GREB1L genes accurately reflects historical (pre-European contact) patterns?
- Prince et al. (2017) concluded that the haplotypes associated with early migration timing evolved only once within each species. Is that the case, or are the genetic variants more evolutionarily labile?

Ford *et al.* 2020



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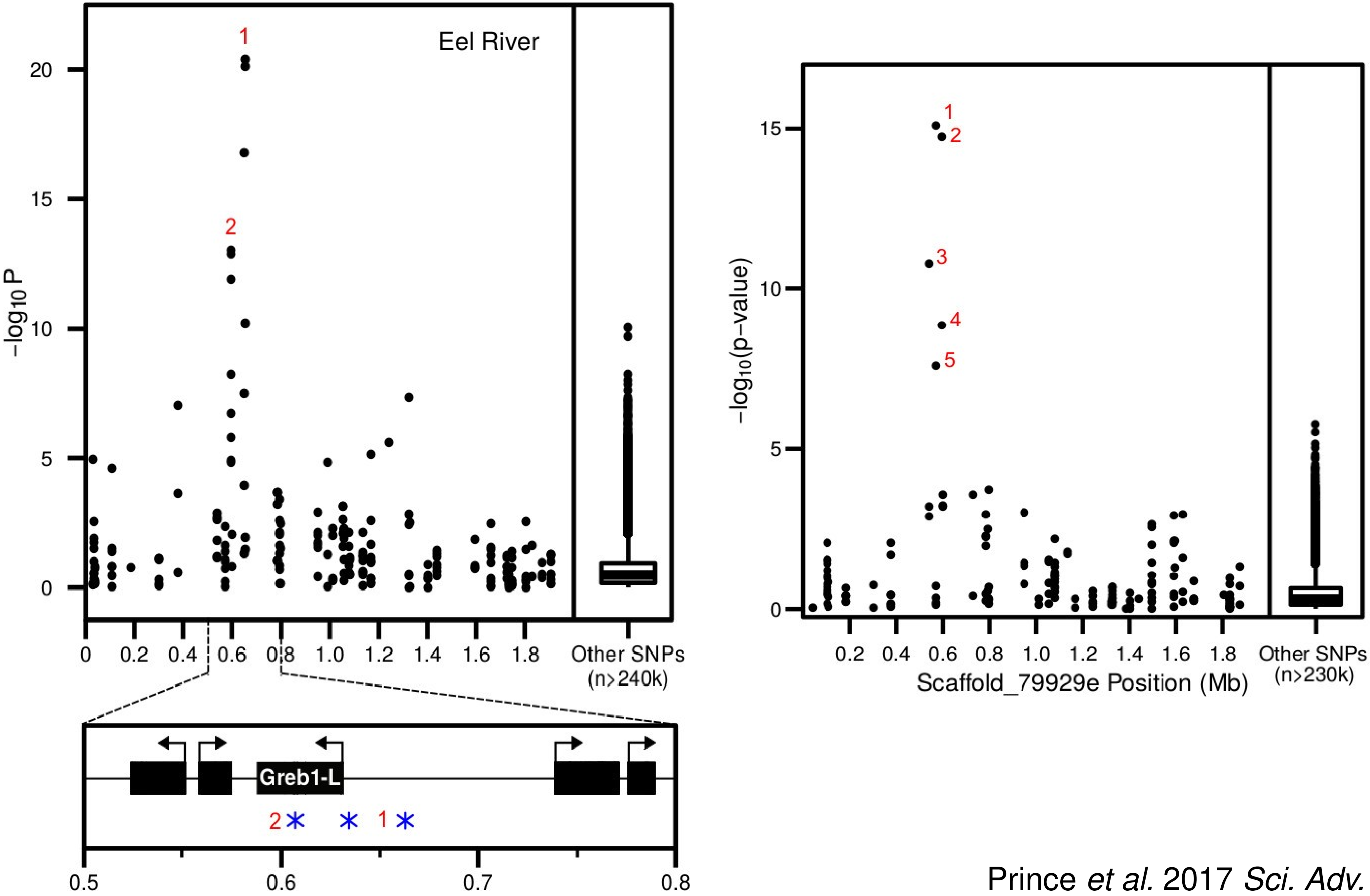
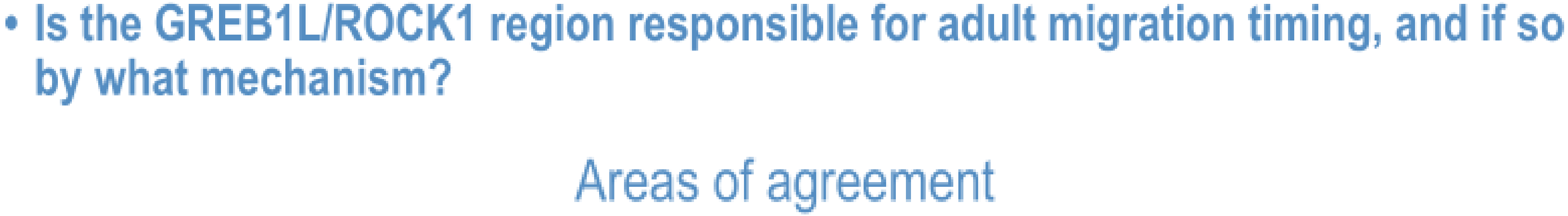
Ford *et al.* 2020

The same single genetic region is associated with run-timing in both Chinook and steelhead.



Prince *et al.* 2017 *Sci. Adv.*

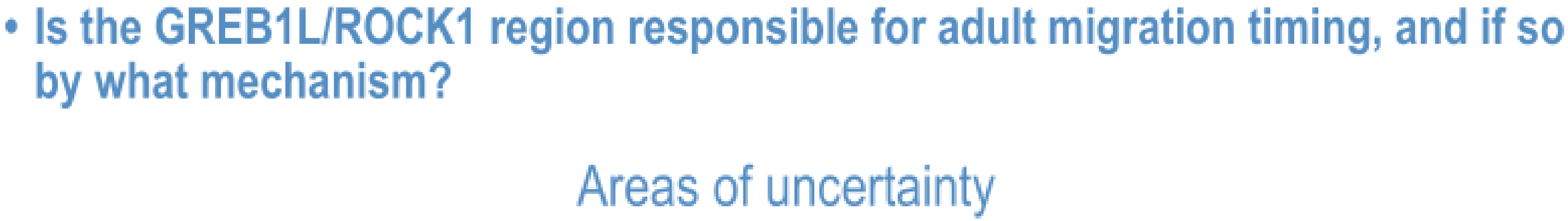


- **Is the GREB1L/ROCK1 region responsible for adult migration timing, and if so by what mechanism?**

Areas of agreement

"Based on both published and unpublished data, multiple studies have identified one ~200 Kb region of chromosome 28 (near two genes called GREB1L and ROCK1) with alleles strongly associated with various measures of adult run timing in multiple populations of Chinook salmon and steelhead. The populations examined range from coastal populations in California and Oregon, to interior Columbia River, to the Straits of Juan de Fuca and Puget Sound."

Ford *et al.* 2020

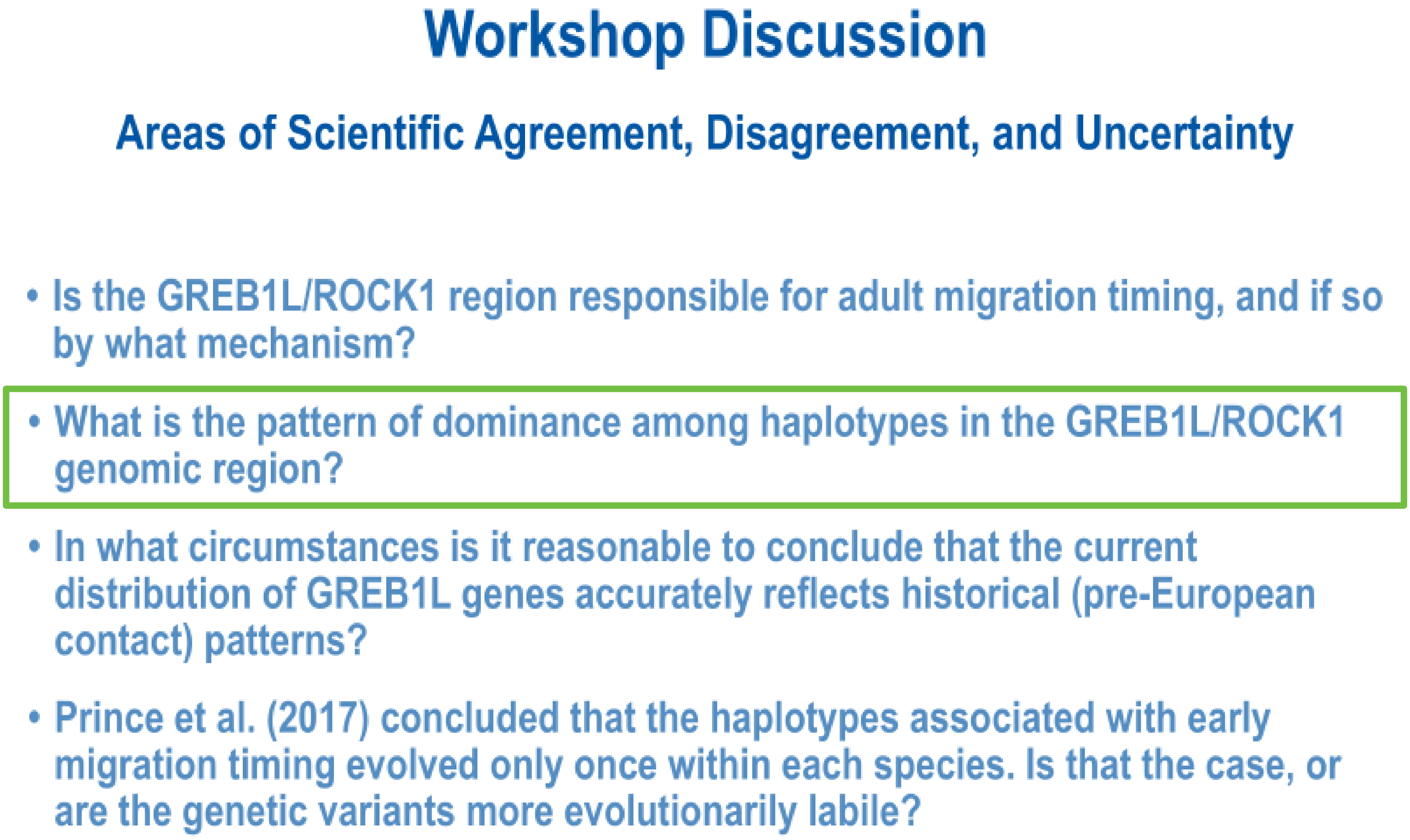


- Is the GREB1L/ROCK1 region responsible for adult migration timing, and if so by what mechanism?

Areas of uncertainty

“The primary uncertainty related to this question is that the causal variants within the region remain unknown... Based on the studies to date, it is nearly certain that the GREB1L/ ROCK1 region contains causal variants, but there are numerous SNPs within this region, most of which are likely to be neutral with respect to the physiology of run timing and only associated through linkage.”

Ford *et al.* 2020



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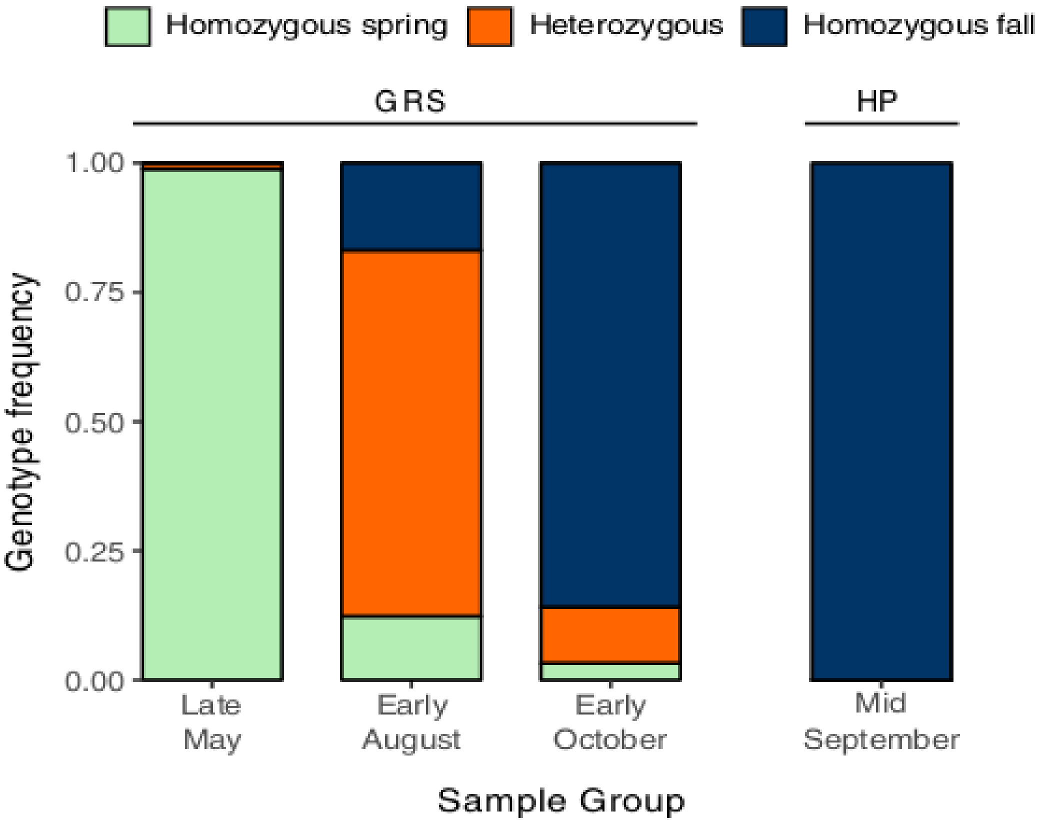
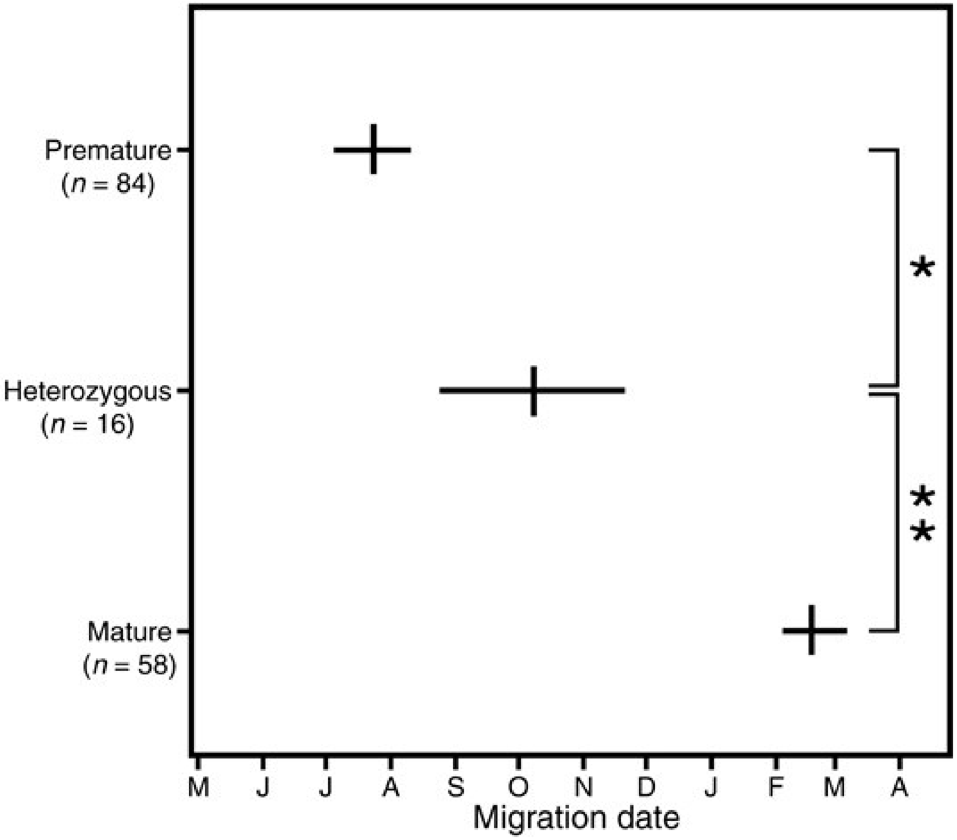
Ford *et al.* 2020

Heterozygotes (e.g., individuals with one spring variant and one fall variant) have an intermediate migration timing.

Thompson *et al.* 2019 *PNAS*





Prince *et al.* 2017 *Sci. Adv.*

- What is the pattern of dominance among haplotypes in the GREB1L/ROCK1 genomic region?

Areas of agreement

“The workshop participants agreed that understanding the dominance patterns for run-timing variation associated with the GREB1L/ROCK1 region is important for evaluating the likely persistence of the ‘early’ allele(s) if environmental conditions favor late run timing… For Chinook salmon, the empirical data so far appear to be consistent with either an additive model or dominance of the early allele. No existing data sets have found strong evidence that the early phenotype is recessive. In addition, in some coastal locations where spring-run Chinook have been largely extirpated (Shasta River, Scott River, Iron Gate, and Wynoochee Rivers) or were never known to exist (Eel River?), the early alleles are absent or extremely rare (Thompson et al. 2019), which would not be expected if the premature allele were recessive.”

Ford *et al.* 2020

- What is the pattern of dominance among haplotypes in the GREB1L/ROCK1 genomic region?

Areas of uncertainty

“It may be too simplistic to focus on dominance of migration timing alone since genetic variation at the GREB1L/ROCK1 region also could influence other traits that are more difficult to study. In addition, it seems likely that successful expression of the spring/early run time phenotype requires a host of additional adaptations, such as appropriate egg and juvenile growth regimes for the upstream habitats and that the genetic basis of these adaptations has not been characterized.”

Ford *et al.* 2020

Workshop Discussion

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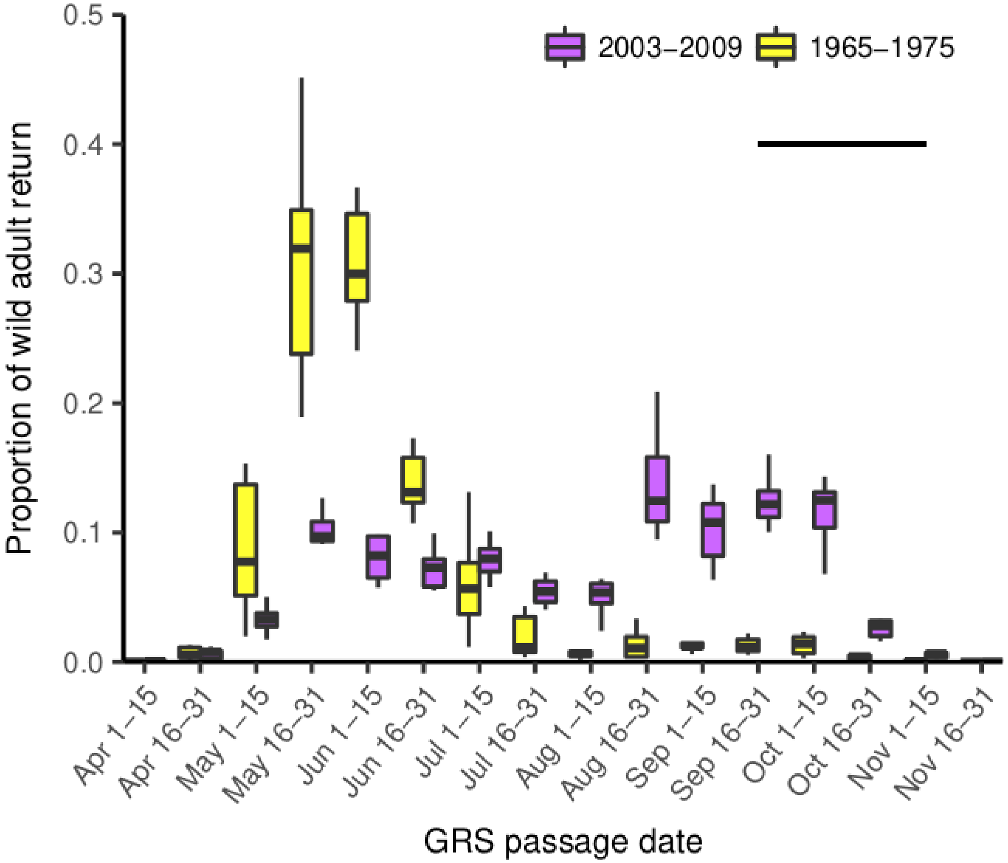
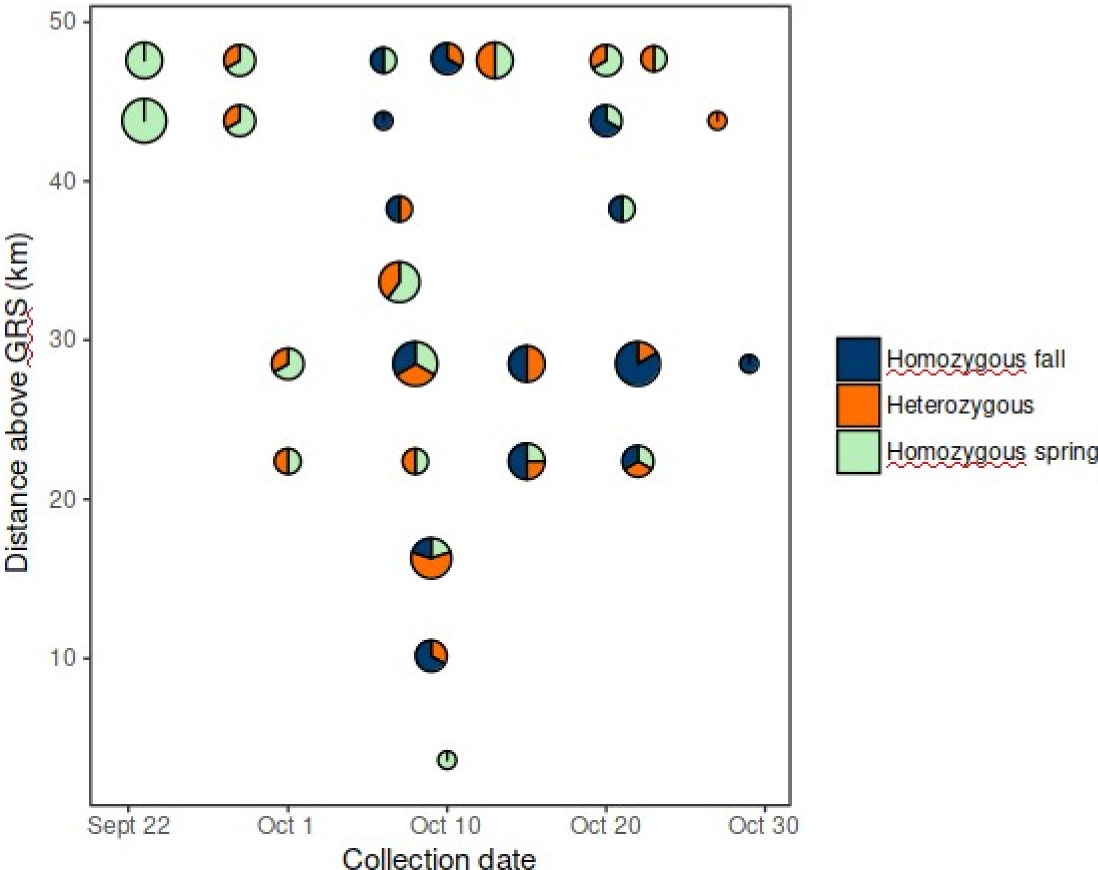
Ford *et al.* 2020

Anthropogenic activities have increased interbreeding between spring and fall Chinook in many locations.





Thompson *et al.* 2019 *PNAS*

- In what circumstances is it reasonable to conclude that the current distribution of GREB1L genes accurately reflects historical (pre-European contact) patterns?

Areas of agreement

“Workshop participants agreed that some interbreeding between spring and fall coastal Chinook salmon certainly occurred naturally, but that the degree of interbreeding in many coastal areas has likely increased over the past 100 years as spring run have declined and habitat alterations and other human actions have increased the potential for spawning overlap between spring and fall runs.”

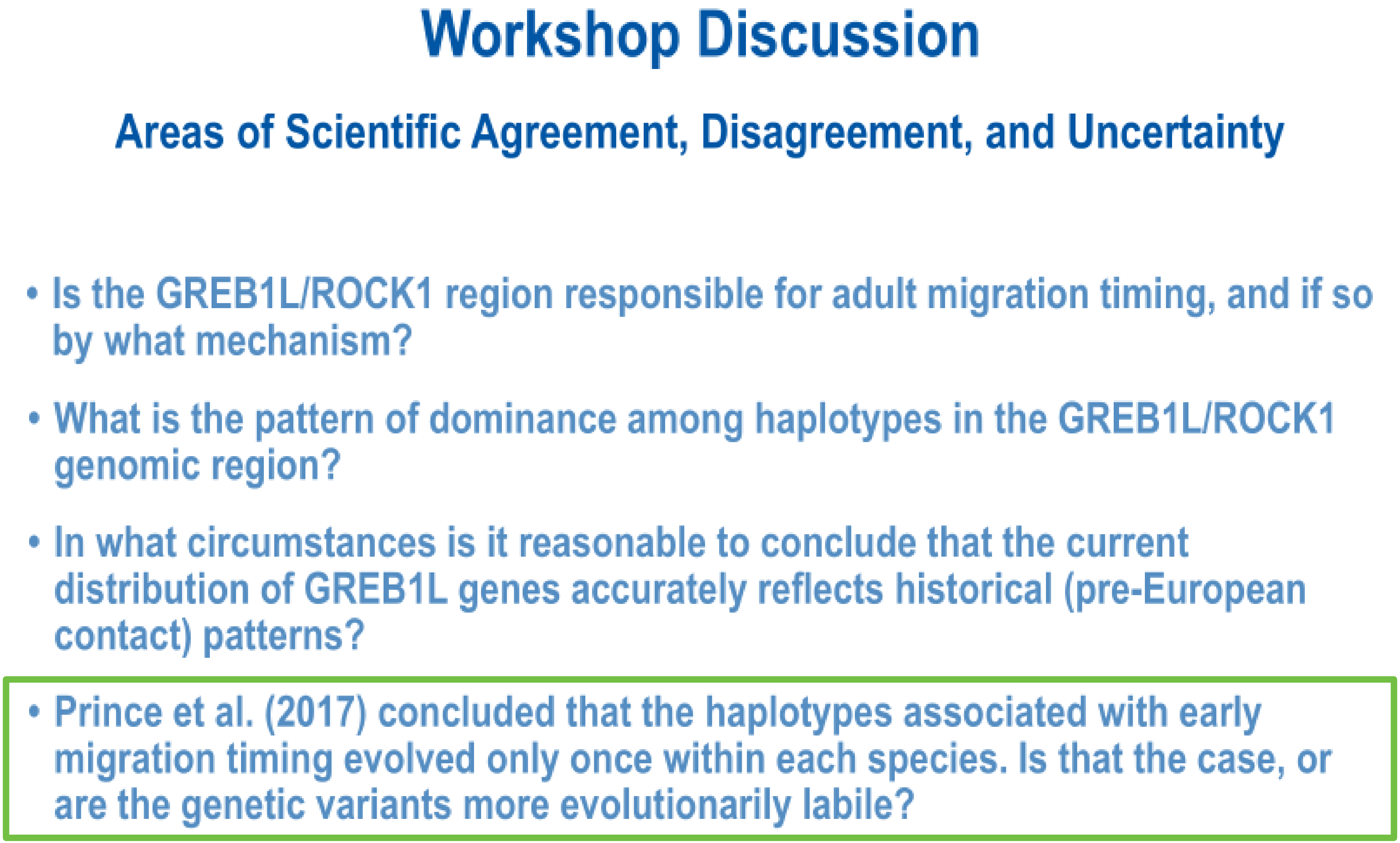
Ford *et al.* 2020

- In what circumstances is it reasonable to conclude that the current distribution of GREB1L genes accurately reflects historical (pre-European contact) patterns?

Areas of uncertainty

“It is unclear how much demographic isolation from fall run is required for spring Chinook salmon to persist.”

Ford *et al.* 2020



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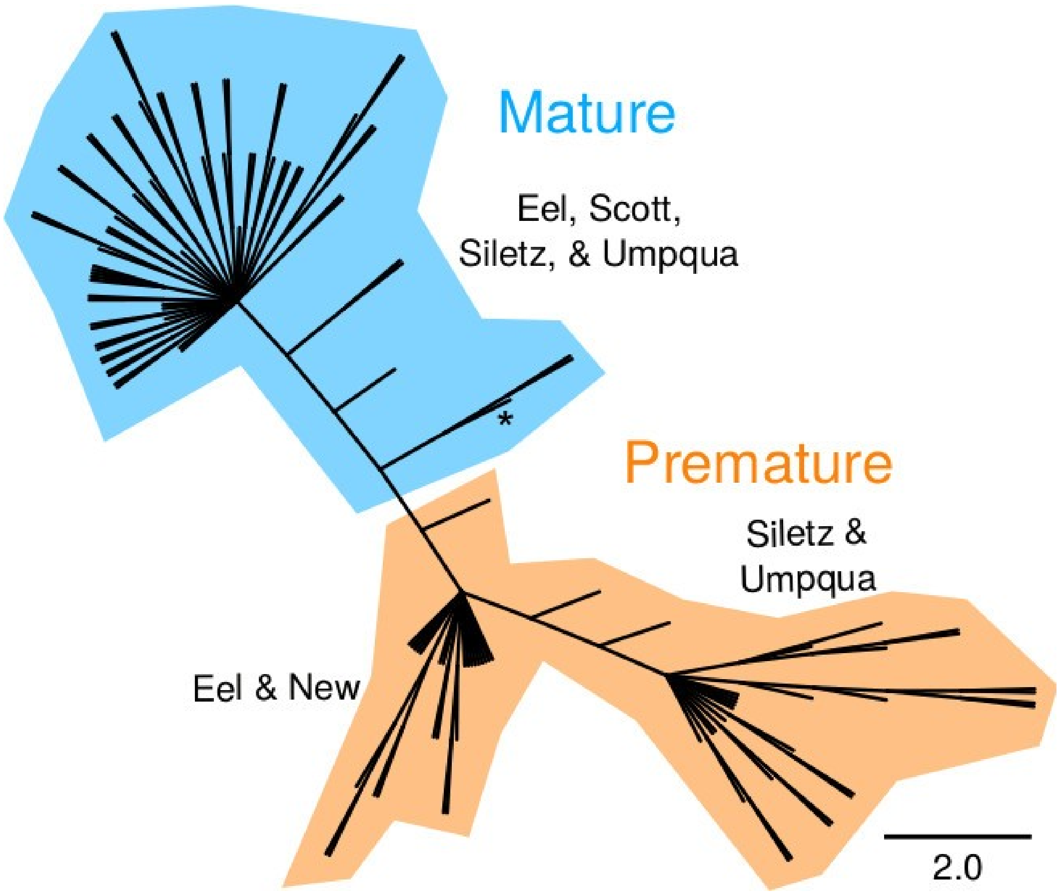
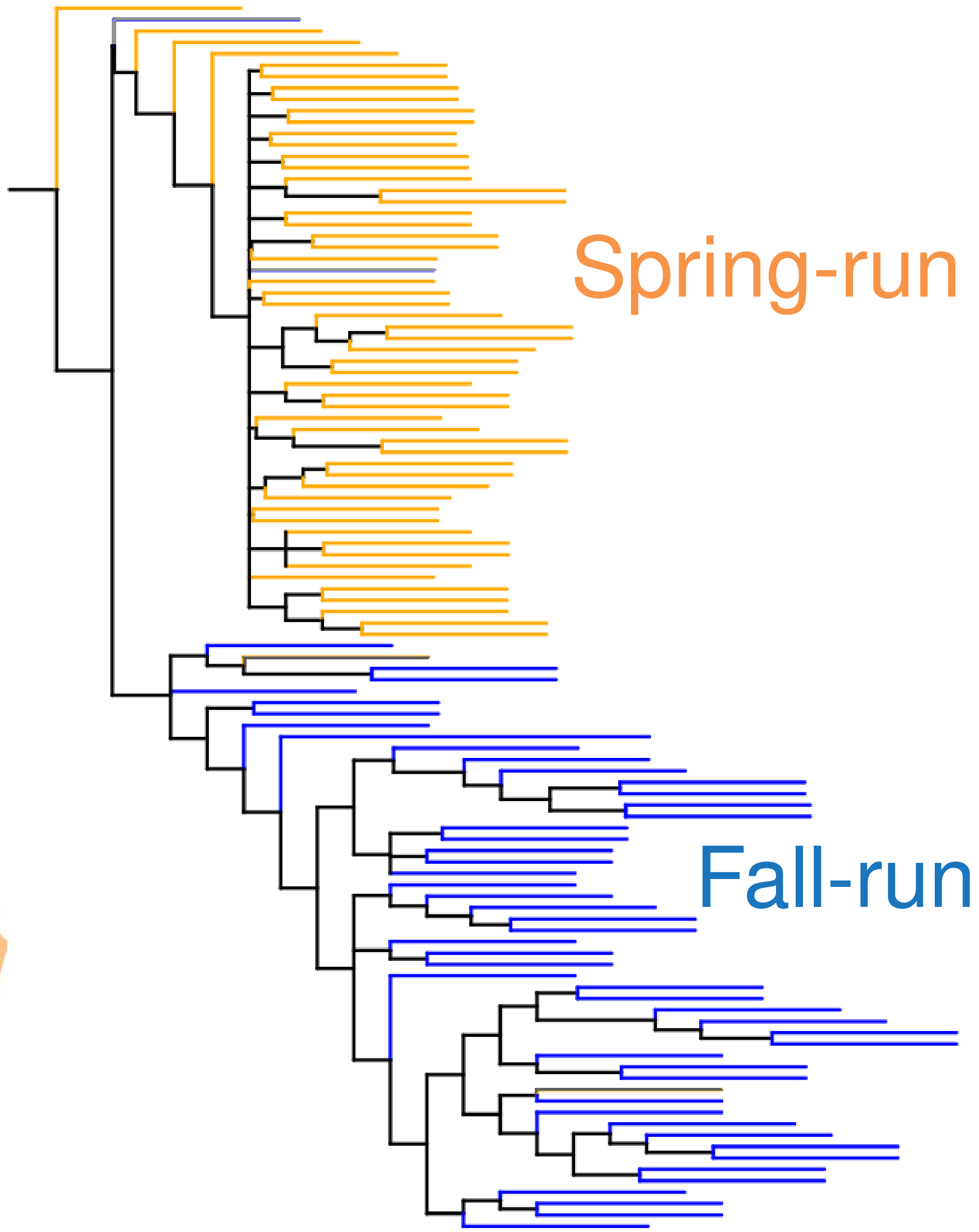
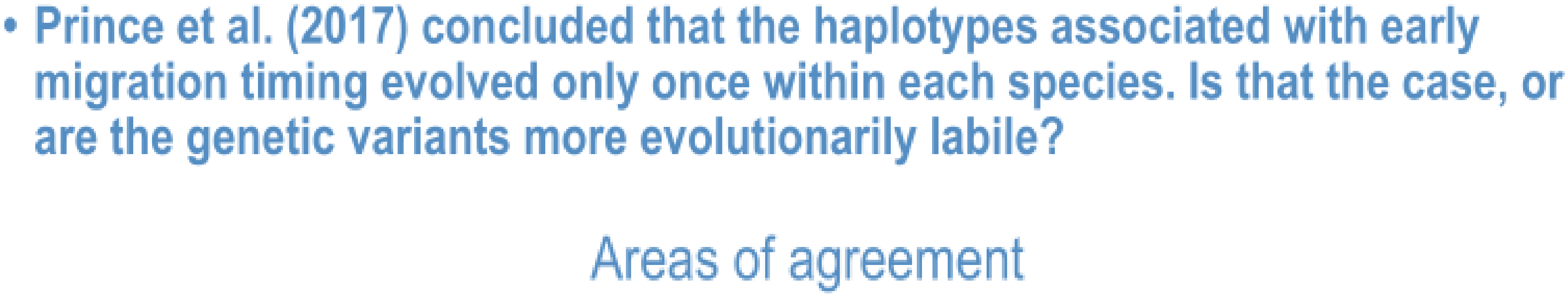
Ford *et al.* 2020

A single ancient allelic evolutionary event is the ultimate source of all spring-run alleles.





Prince *et al.* 2017 *Sci. Adv.*



- Prince et al. (2017) concluded that the haplotypes associated with early migration timing evolved only once within each species. Is that the case, or are the genetic variants more evolutionarily labile?

Areas of agreement

“The evolutionary history of the GREB1L/ROCK1 region is complex and has not been well characterized throughout each species’ entire range. But it is clear that the early and late haplotypes that have been well characterized evolved long ago in each species’ evolutionary history. It is also clear, based on available data, that the allelic variants for early migration have not arisen independently via new mutations from the genomic background of late migration individuals in each watershed.”

Ford *et al.* 2020

- **Prince et al. (2017) concluded that the haplotypes associated with early migration timing evolved only once within each species. Is that the case, or are the genetic variants more evolutionarily labile?**

Areas of uncertainty

Ford *et al.* 2020

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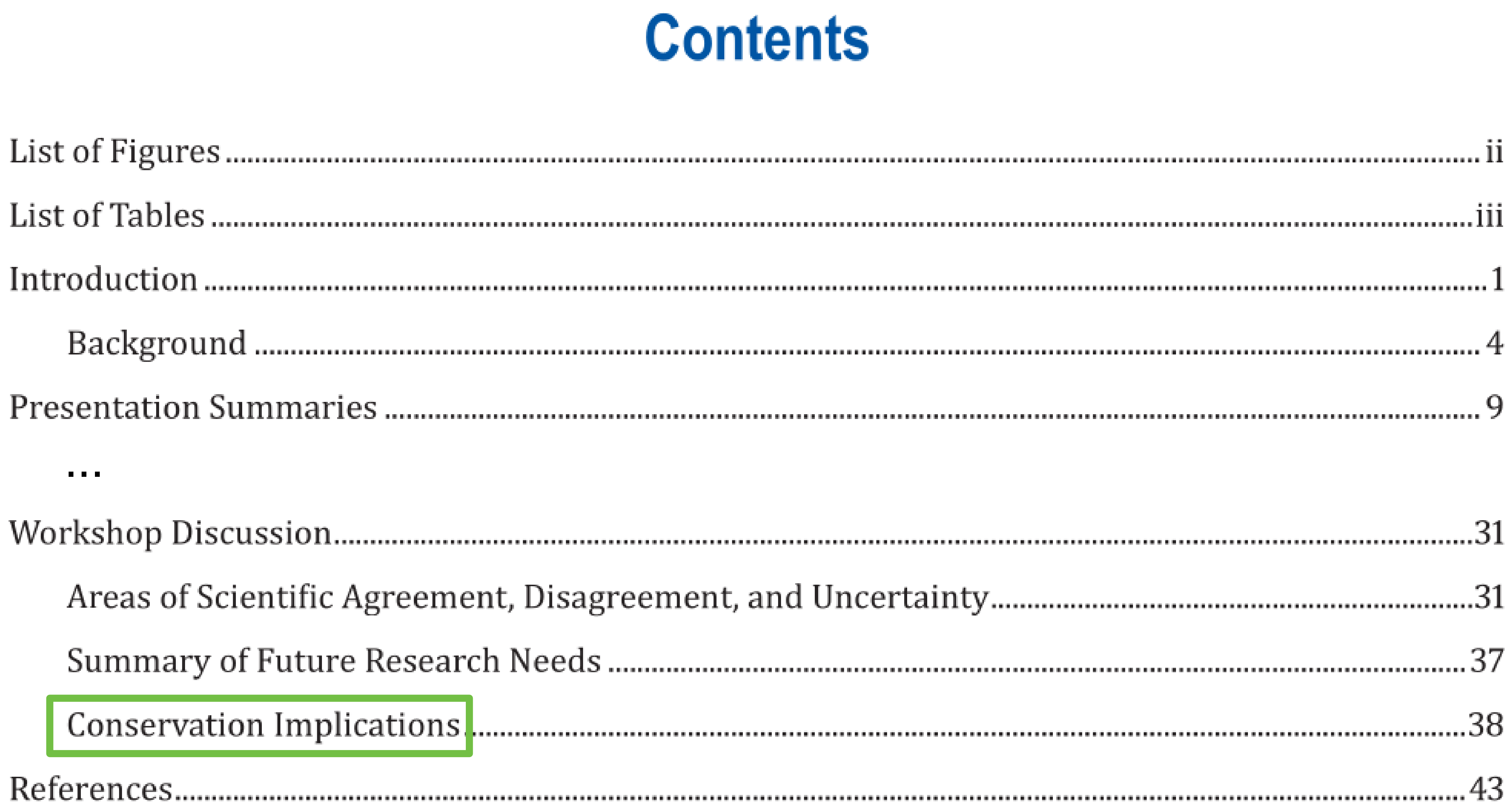

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Ford *et al.* 2020

Conservation Implications

Areas of agreement

“The workshop participants agreed that spring Chinook salmon and summer steelhead occupy a specialized ecological niche that has made them particularly vulnerable to extirpation or decline due to habitat degradation. The participants also agreed that diversity, including diversity in adult run timing, is important for the long-term viability of many if not all salmon ESUs.”

Ford *et al.* 2020

Conservation Implications

Areas of agreement

“The participants generally agreed that the finding that the early run trait has a simple genetic basis implies that it is at greater risk of loss than if it were highly polygenic because loss of the ‘early’ allele(s) equates to the loss of the phenotype. The exception to this conclusion would be if fish containing the early allele could readily migrate from a reservoir elsewhere, either from another population within an ESU or from a different ESU, and successfully reproduce in the new location.”

Ford *et al.* 2020

Conservation Implications

Areas of agreement

“The reduction in frequency of the spring-run trait in multiple coastal Chinook salmon ESUs may therefore be an indicator of greater risk to spring run in each ESU than would be the case if the allele were common in multiple ESUs. If spring-run populations are at risk in multiple ESUs, this is therefore something that should be considered in evaluating risk.”

Ford *et al.* 2020

Conservation Implications

Areas of agreement

“The participants generally agreed that the evaluation of risk to early returning population groups (spring Chinook, summer steelhead) needs to consider what we now know about the genetic basis of adult return time.”

“The participants generally agreed that using patterns of genetic variation throughout the genome remains important for identifying conservation units, rather than identifying units based solely on small genomic regions associated with specific traits.”

Ford *et al.* 2020

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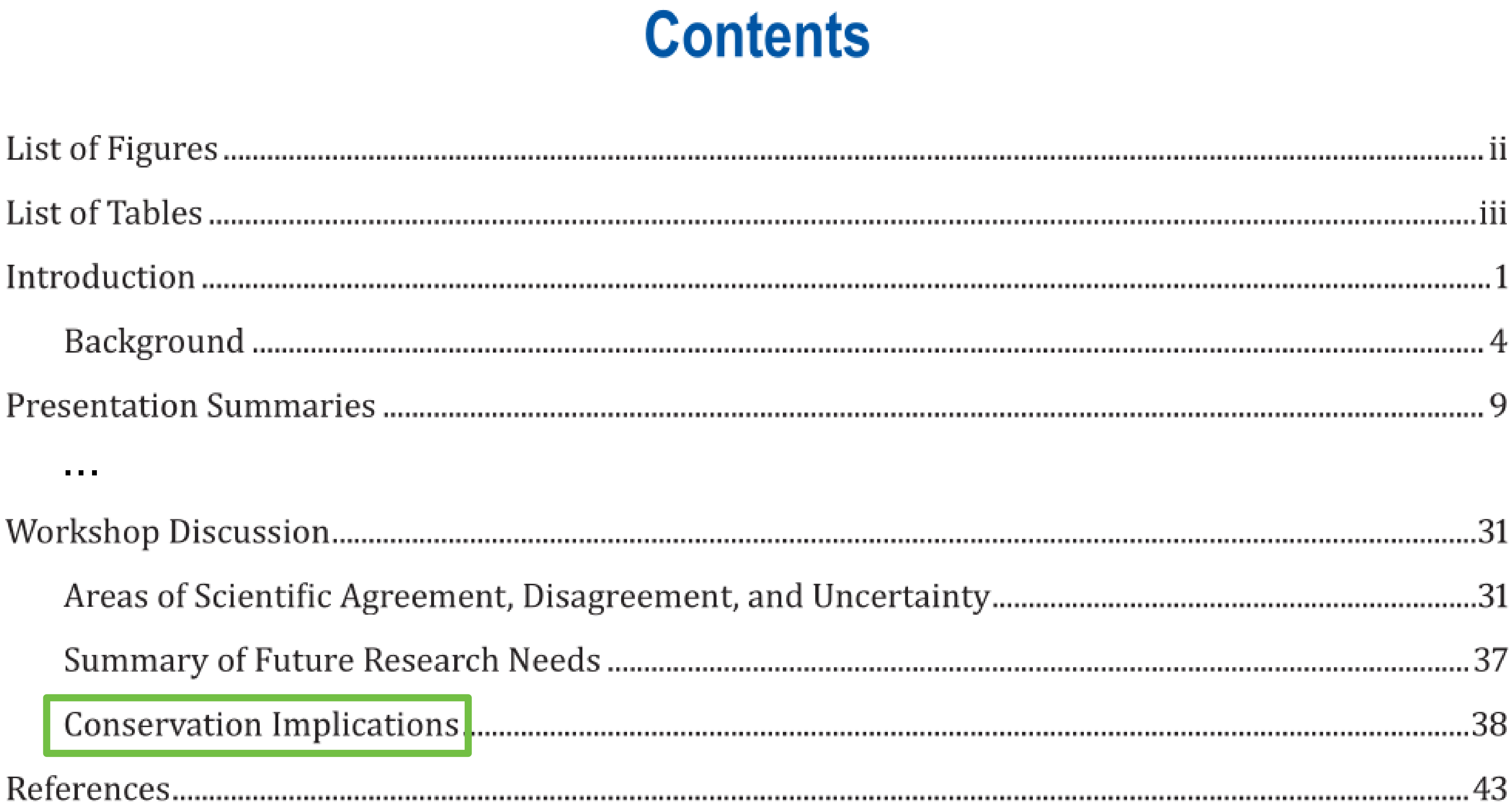

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Ford *et al.* 2020

Conservation Implications

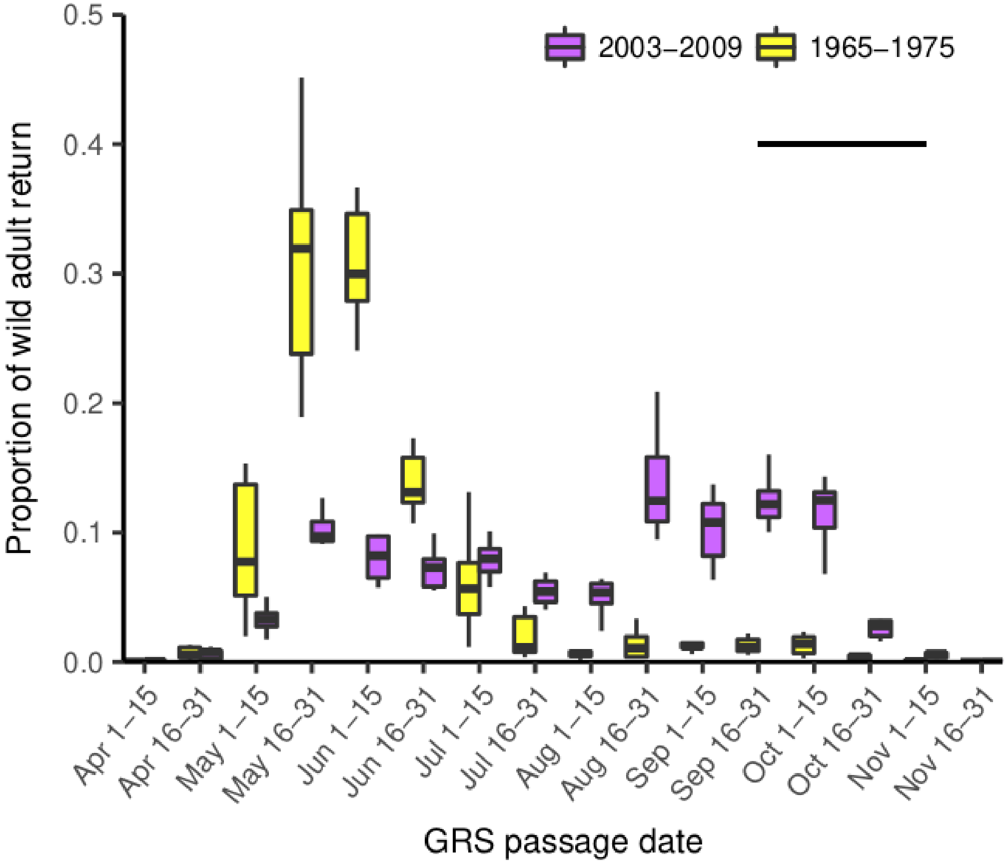
Areas of uncertainty

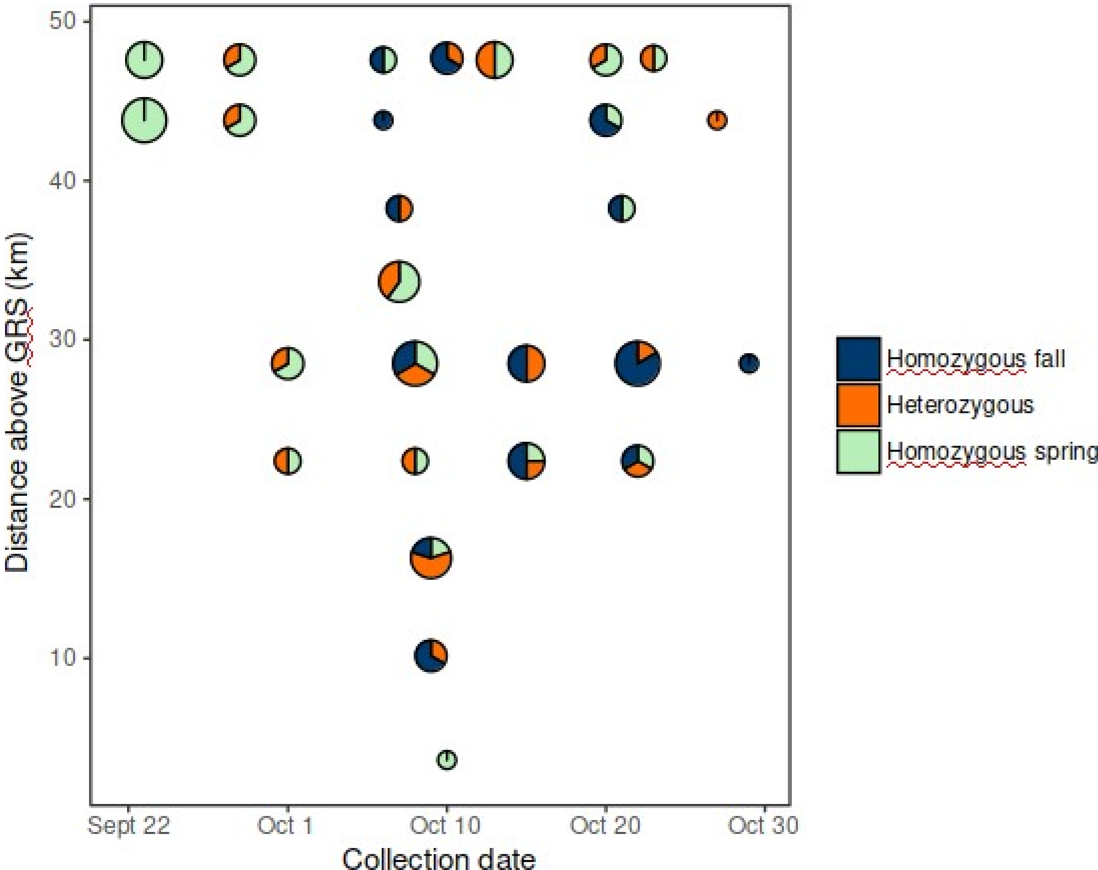
“One area of uncertainty and potential disagreement at the workshop was the degree to which run-timing diversity in spring Chinook salmon is partitioned among populations versus among individuals within a population.”

“The extent to which observed contemporary levels of interbreeding between individuals with early and late run timing would be typical under historical environmental conditions is unknown.”

Ford *et al.* 2020

Anthropogenic activities have increased interbreeding between spring and fall Chinook in many locations.





Thompson *et al.* 2019 *PNAS*

Conservation Implications

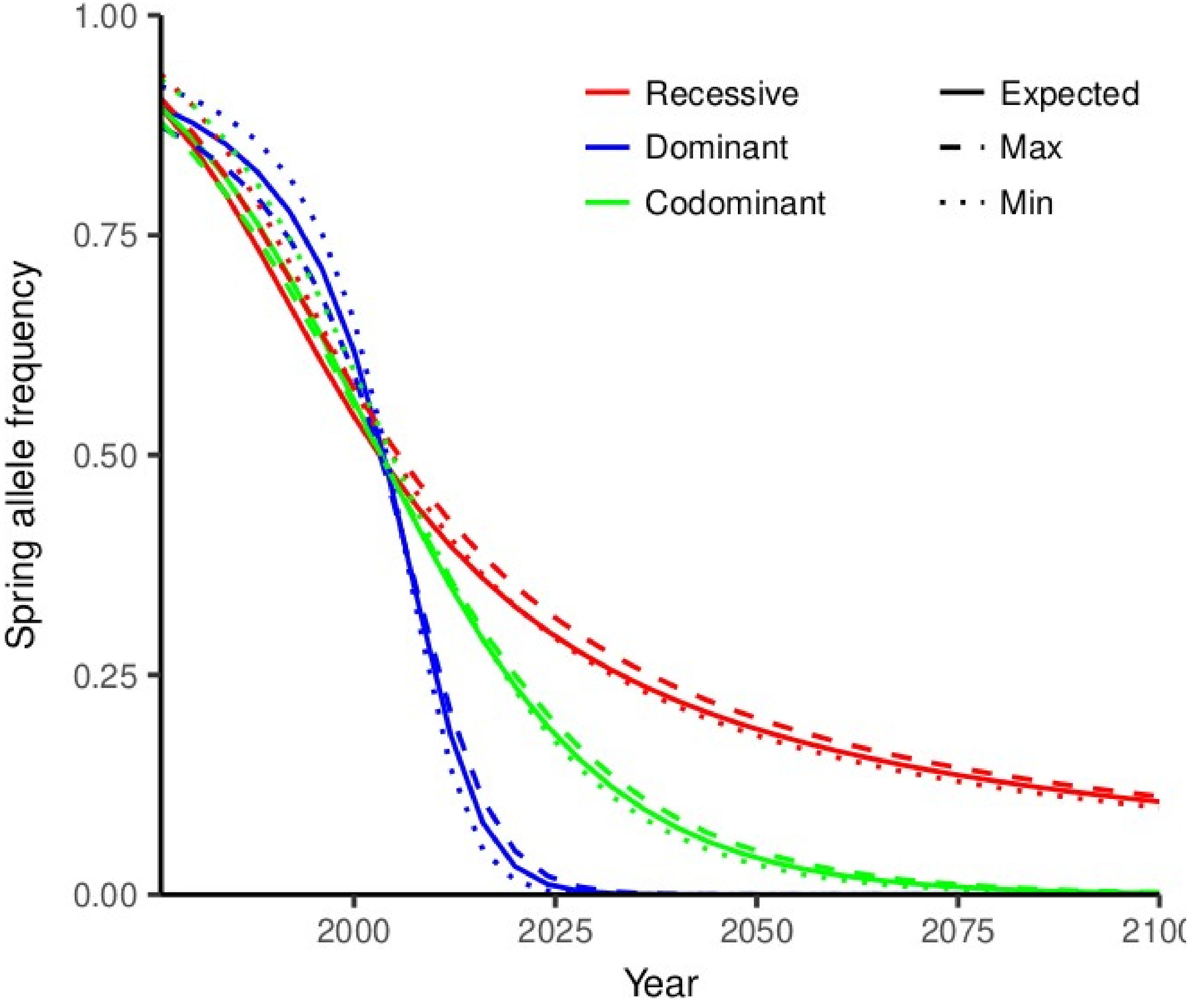
Areas of uncertainty

“Understanding the conservation implications of dominance patterns at the GREB1L/ROCK region is also important and is complicated because of tradeoffs between the probability of persistence of the early-run allele and the feasibility of starting new early-run populations.”

“The dominance-recessive relationships might influence the success of colonization events.”

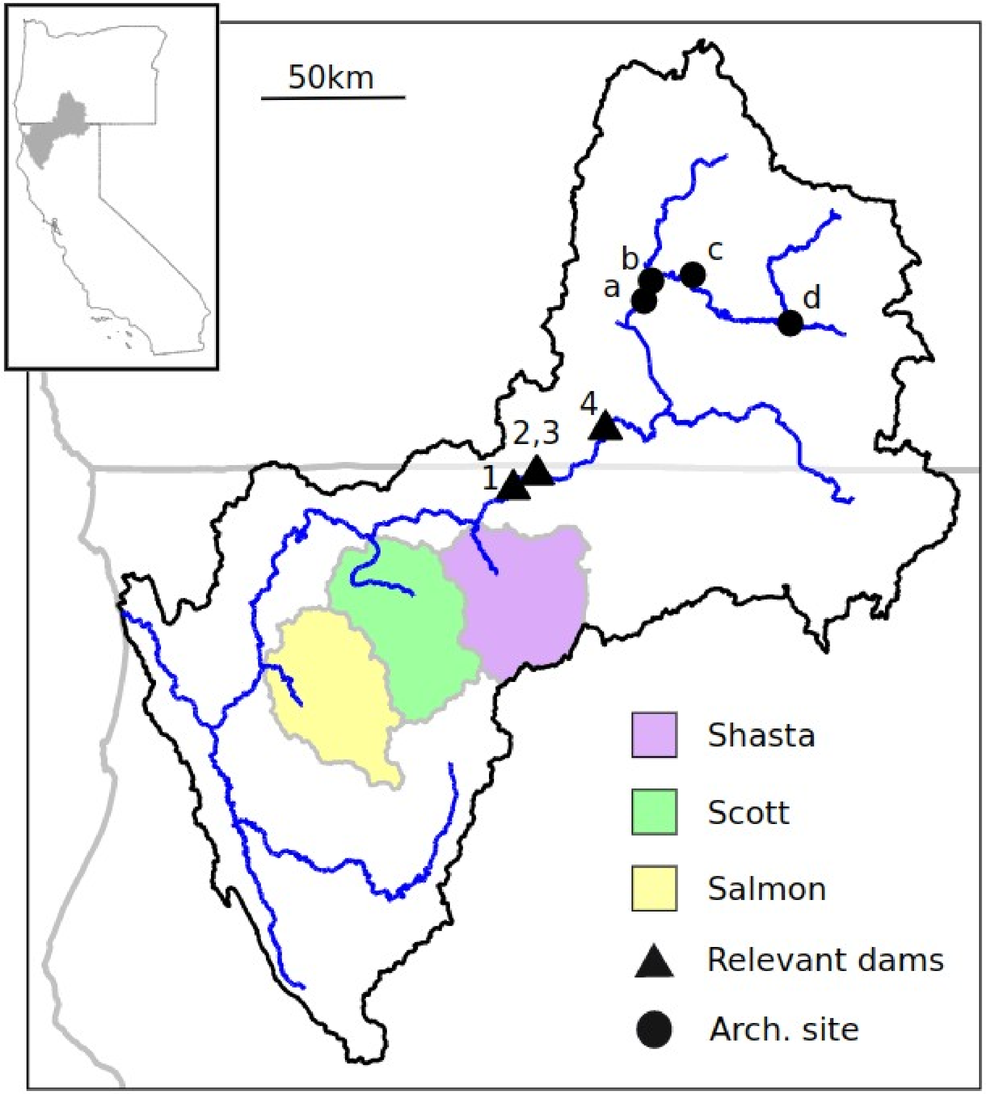
Ford *et al.* 2020

If recessive, the spring-run would persist at a relative high frequency, even in the absence of the spring-run phenotype.



Thompson *et al.* 2019 *PNAS*

The Shasta and Scott Rivers are not serving as sustainable reservoirs of the spring-run allele.



Location	Date spring Chinook last observed	Number of samples	Spring-run allele frequency
Salmon	present	116	0.20
Shasta	1930's	440	**0.002**
Scott	1970's	432	**0.002**

Thompson *et al.* 2019 *PNAS*

Conservation Implications

Areas of uncertainty

“Regardless to what extent current levels of interbreeding are a consequence of human mediated habitat alterations, such interbreeding and the common occurrence of heterozygotes at the GREB1L/ROCK1 region presents challenges for status monitoring, recovery planning, and other management actions.”

“Improved strategies are needed for monitoring run timing and associated genetic variation… Based on presentations of genotype surveys in several watersheds (Klamath, Rogue, Chehalis) containing both spring and fall-run Chinook salmon, monitoring trends in GREB1L/ROCK1 genotypes might provide a more accurate measure of spring run relative abundance than phenotypic monitoring.”

Ford *et al.* 2020

Conservation Implications

Areas of uncertainty

“Conservation measures for spring run that were discussed included potentially shaping fisheries to focus disproportionately on fish with fall run timing, restoring access to spring-run habitat that has been blocked, considering restoring natural barriers that have been modified to increase fall-run access to historically spring-run habitats, and restoring more natural flow regimes (e.g., low summer flows that prevent mature migrating individuals from encroaching on premature habitat).”

Ford *et al.* 2020

Reviewing and Synthesizing the State of the Science Regarding Associations between Adult Run Timing and Specific Genotypes in Chinook Salmon and Steelhead: Report of a workshop held in Seattle, Washington, 27–28 February 2020

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June 2020