A paradigm revisited: cutthroat trout, rainbow trout, and the nature of hybridization

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McKelvey KS, Young MK, Wilcox TM, Bingham DM, Pilgrim KL, Schwartz MK (2016) Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams. Ecology and Evolution.

Hybridization in fishes

- Common
  - Hybrid zones
  - Meet, mate, and produce offspring
- Causes
  - External fertilization
  - Incomplete reproductive isolation
  - **Persists despite millions of years of divergence**
- Consequences
  - Non-introgressive
  - Introgressive

Our case: cutthroat trout & rainbow trout

- Causes
  - Sister species (diverged 2–10 MY)
  - Fluvial, spring spawners
  - **Extensive stocking of RT (400 million in MT)**
- Introgressive → **Hybrid swarm**

Cott & Mochnacz 2007

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The hybrid swarm

- Definition
  - Parental fish absent
  - Parental genes randomly distributed

- Inevitable?
  - The hybrid ratchet (Epifanio & Philipp 2001)
  - Any hybridization = all hybridized
  - Genomic extinction

Campton & Utter 1985

Young et al. 2001: "Hybridization with completely random mating and little or no viability decrease in the hybrids compared with the parental species frequently occurs following secondary contact between rainbow trout and nearly all cutthroat trout subspecies."

Docker et al. 2003: "Hybridization and extensive introgression will destroy the genetic integrity of the native cutthroat and rainbow trout populations..."

Ostberg & Rodriguez 2004: "Indeed, introduced, non-native resident rainbow trout readily hybridize and form hybrid swarms with native trout..."

Rubidge & Taylor 2004: "...our results suggest that in the absence of management intervention, hybrid swarm formation and local extinctions of pure WCT populations are likely in at least two tributaries...and possibly more..."

Bettles et al. 2005: "[two locations] exhibited a diverse array of recombinant genotypes and very few F1 or pure-type, suggesting that these two systems are hybrid swarms."

Ostberg & Rodriguez 2006: "Typically, when nonnative trout are introduced into areas with cutthroat trout populations, mating structures collapse and hybrid swarms form...The probable outlook for WCT within the Stehekin River drainage...is population decline coupled with increasing introgression, leading to the formation of a hybrid swarm."
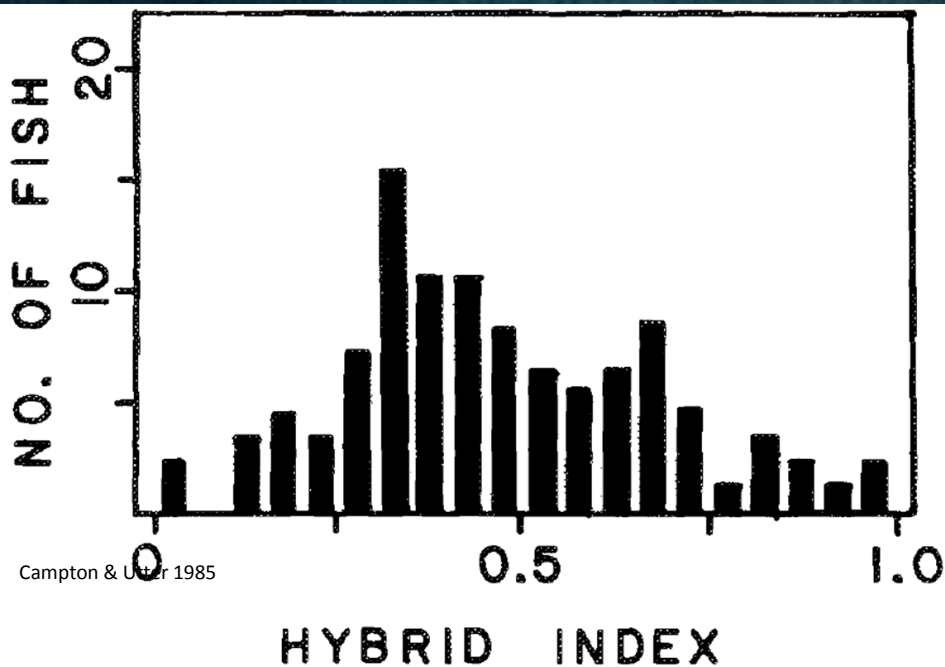
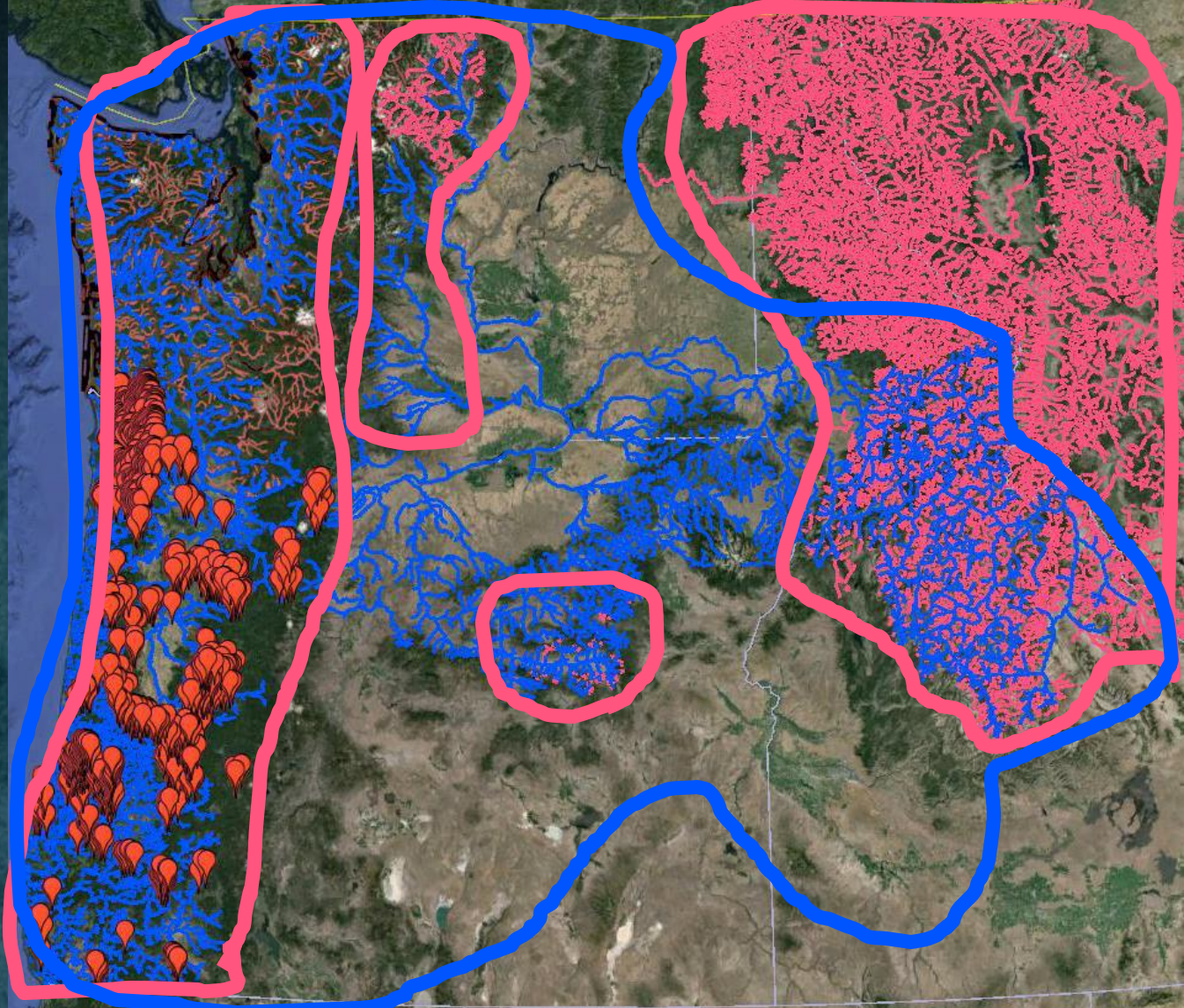# A paradox: different locations, different patterns

Where RT introduced
- Co-occurred ~150 y
- Only isolated populations secure
- Introgression known to be common
- RIM presumed weak

Where RT native
- Co-occurred ~15,000 y
- Population strongholds
- Introgression presumed rare
- RIM presumed strong

Where CT introduced
- CT genes persist

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Literature review: genesis of the hybrid swarm

- Earliest: Hubbs 1955

- Age of allozymes (1981–1991)

- Modest numbers of genetic markers

Species	Source	Sites	Hybrid swarms	Parentals
RT x PCT	Busack & Gall 1981	3	1(?)	2
RT x CCT	Campton & Utter 1985	13	2	11
YCT x WCT	Gyllensten et al. 1985	2	2	0
RT x LCT	Bartley & Gall 1991	4	0	4
YCT x WCT	Forbes & Allendorf 1991	3	3	0
RT x **CT** x AT	Carmichael et al. 1993	20	2	18

AT, Apache trout; CCT, coastal cutthroat trout; CT, unspecified cutthroat trout; LCT, Lahontan cutthroat trout; PCT, Paiute cutthroat trout; RT, rainbow trout; WCT, westslope cutthroat trout; YCT, Yellowstone cutthroat trout.

Literature review: the crusades

- Follow-up studies involved RT x CT

- Hybrid swarms oft claimed

- Few genetic markers

- ...but of 254 sites with admixture, only 13 with no parental forms

- 10 of 13 involve hybridization with other cutthroat trout

| Species	Source	Sites	Hybrid swarms	Parentals
RT x CCT	Young et al. 2001	16	0	16
RT x CCT	Docker et al. 2003	10	0	10
RT x CCT	Ostberg & Rodriguez 2004	7	0	7
RT x LCT	Peacock & Kirchoff 2004	4	1	3
RT x WCT	Rubidge & Taylor 2004	18	0	18
RT x CCT	Baumsteiger et al. 2005	3	0	3
RT x CCT	Bettles et al. 2005	13	0	13
RT x WCT	Ostberg & Rodriguez 2006	18	0	18
RT x WCT	Kozfkay et al. 2007	17	0	17
RT x CCT	Williams et al. 2007	24	0	24
RT x WCT	Boyer et al. 2008	31	1(?)	30
RT x YCT	Gunnell et al. 2008	28	0	28
RT x WCT	Bennett et al. 2009	42	0	42
RT x CCT	Heath et al. 2009	36	0	36
RT x WCT	Muhlfeld et al. 2009	1	0	1
RT x WCT	Muhlfeld et al. 2009	35	1(?)	34
RT x YCT	Kovach et al. 2011	15	0	15
WCT x RT	Neville et al. 2011	14	0	14
RT x CCT	Buehrens et al. 2012	35	0	35
RT x WCT	Ostberg & Chase 2012	20	0	20
RT x WCT	Rasmussen et al. 2012	23	3(?)	20
RT x WCT	Loxterman et al. 2014	32	0	32

Field test: PIBO streams

- Sampled 188 sites within historical range of WCT
    - RT native in the Clearwater & Kootenai
    - 51 streams with paired sites

- Samples (2–30 per site, 3884 overall)

- Used diagnostic panel of 86 SNPs for WCT, RT, & YCT
    - 106—172 alleles per individual
    - Uncertainty about "diagnosticness"
    - Pure fish: >99% WCT alleles

- Are hybrid swarms common?
    - Two conditions
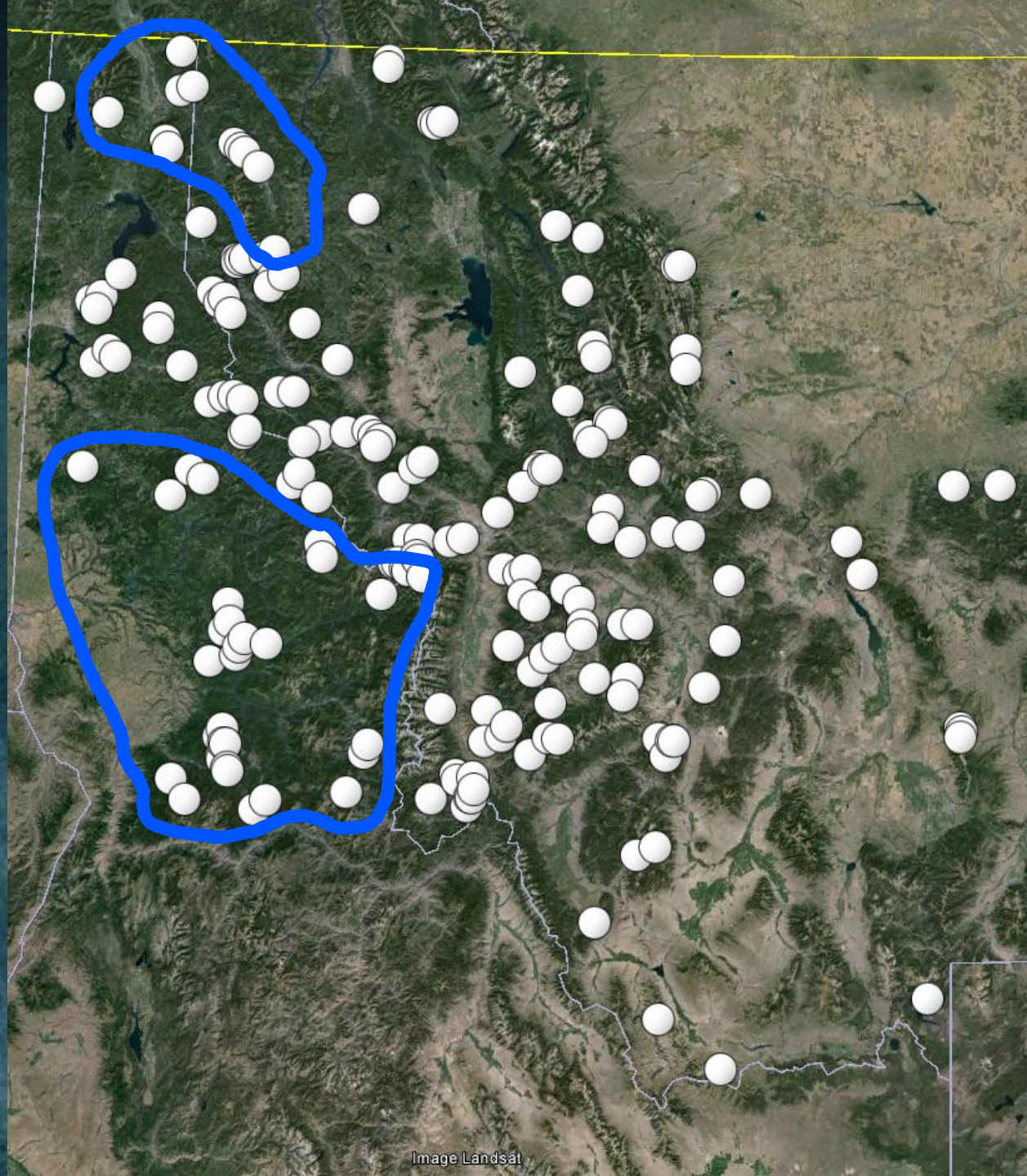
Results

- Most fish are one parental type
  - 72% WCT
  - 4% RT
  - 26% hybrids

- Most sites fail the first condition of HS: parentals are ubiquitous
  - Sites w/ hybrids: 63%
  - Sites w/ parentals: 95%
  - Sites w/ parental WCT: 90%
  - As seen elsewhere

- Initial hybridization rare
 - 33 F_1s (15 from 1 site)
  - As seen elsewhere
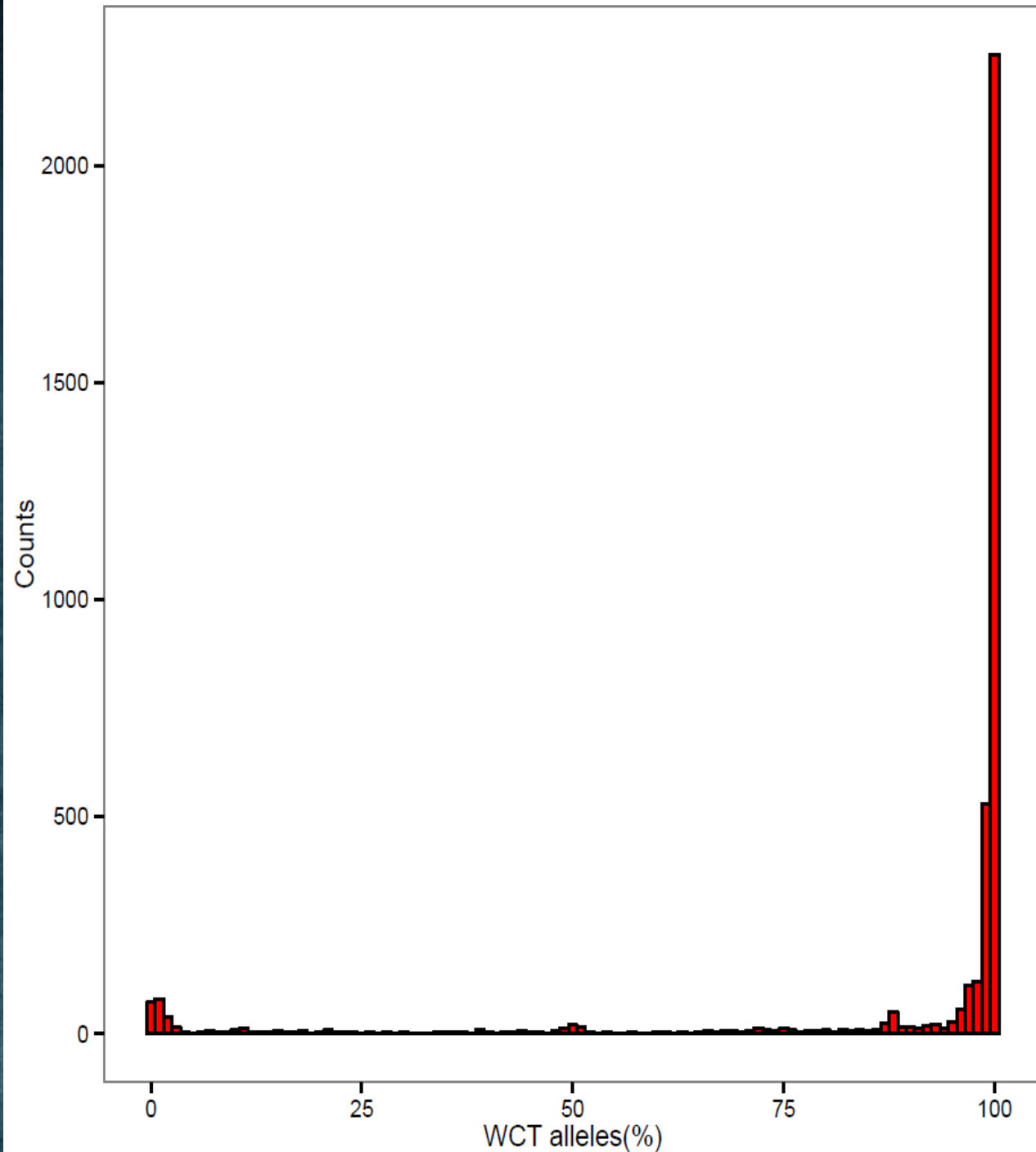
Results

- Most sites fail the second condition of HS : parental genes are not randomly distributed
  - 60% of sites with introgression fail test of allele randomness
  - As introgression declines, statistical power to detect allele distribution ⬇

- Sites with hybrid swarms: 8
  - HS with YCT genes: 7
  - As seen elsewhere

- Hybridization common, but...
  - **Hybrid swarms are not**
  - **They're associated with YCT**
 - **and not inevitable**
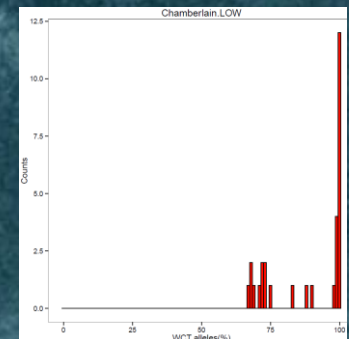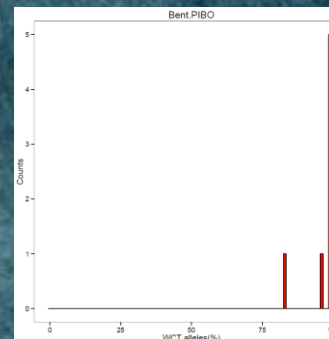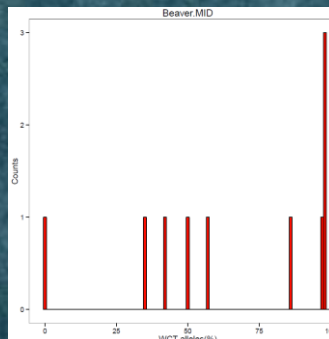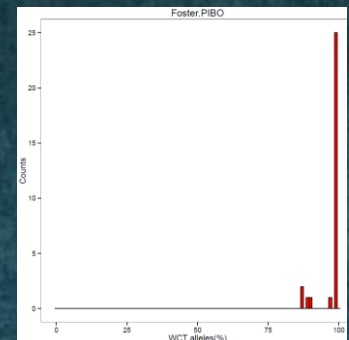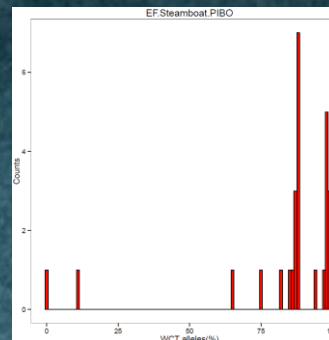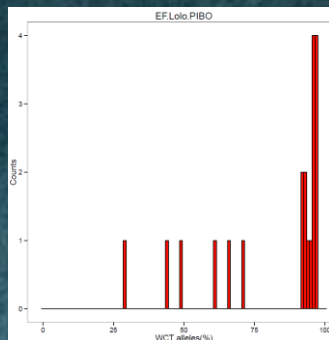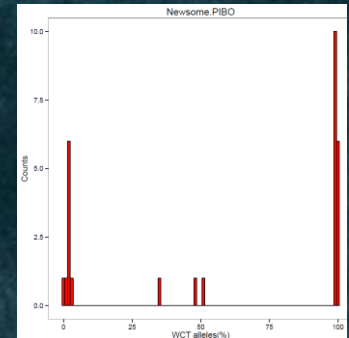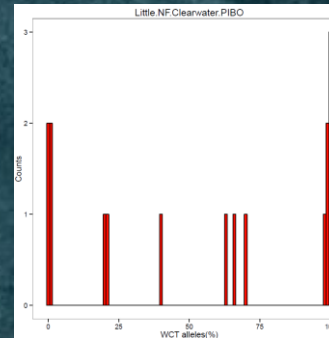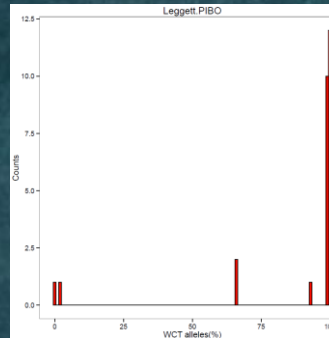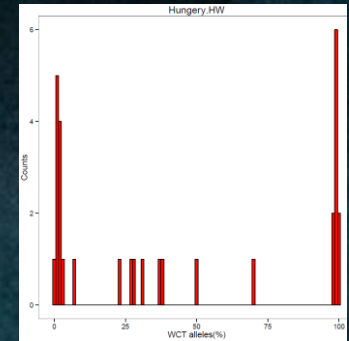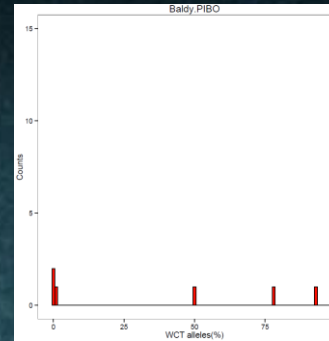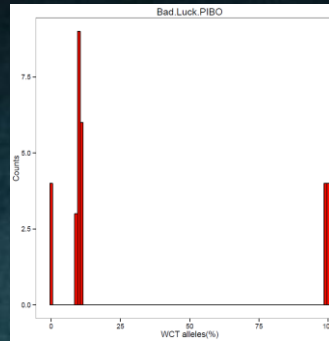
Can introgression be predicted?

- Spatial patterns dominate

- Proxy: Elevation
  - Lower: 23% RT
  - Upper: 4% RT

- Other abiotic influences
  - Temperature
  - Flow

- Biotic influences
  - Propagule pressure
  - RT range?
   - Inside: 33% RT
    - Outside: 12% WCT
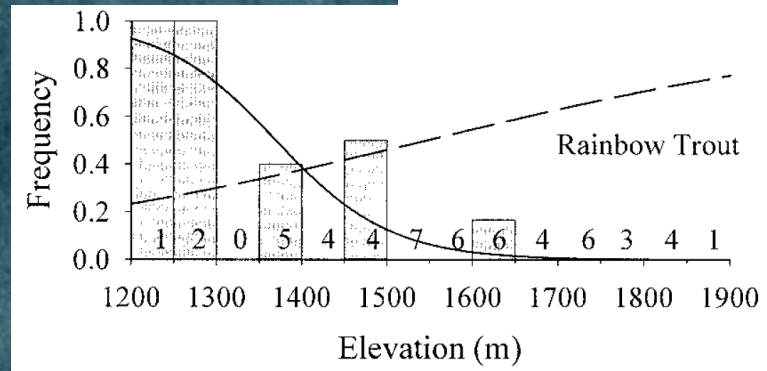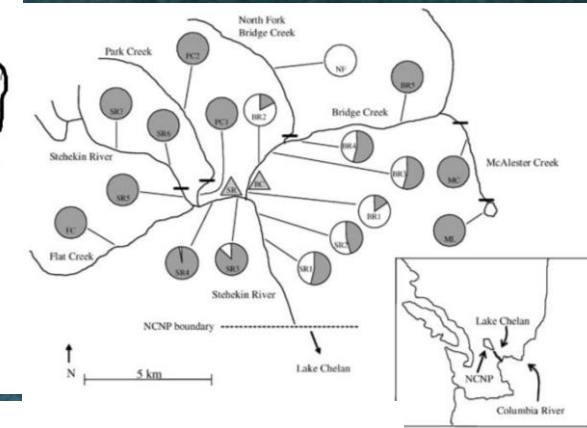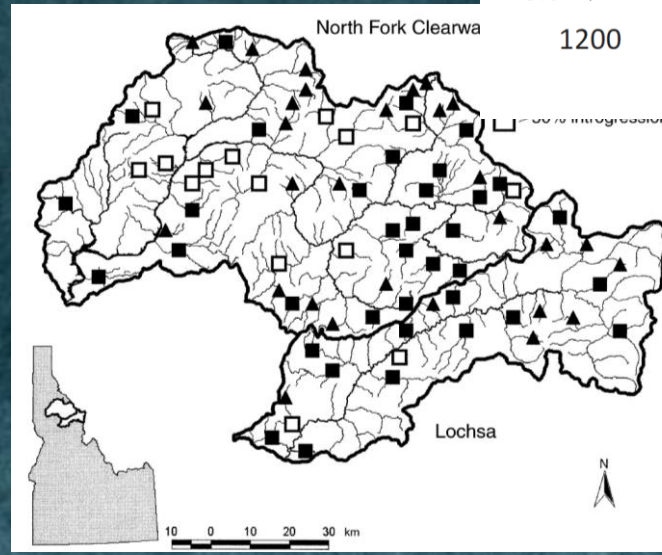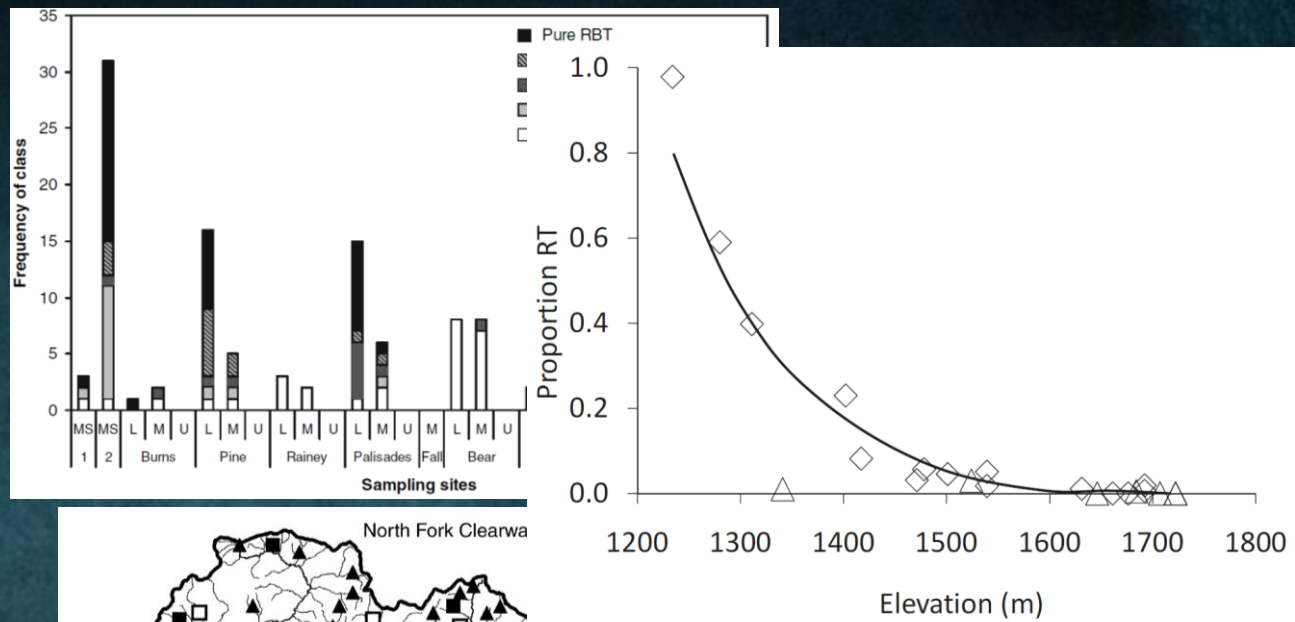
Introgression can be predicted

- Meta-analysis
  - Considered 17 studies
  - ~600 sites throughout W. MT & N. ID within range of WCT

- Dependent variables
  - % RT alleles at a site
  - % of hybrid fish at a site
  - 1%, 10%, 20%

- Final logistic model
  - No spatial correlation in error terms

Legend
- Yes/No
- No/No
- No/Yes
- Yes/Yes
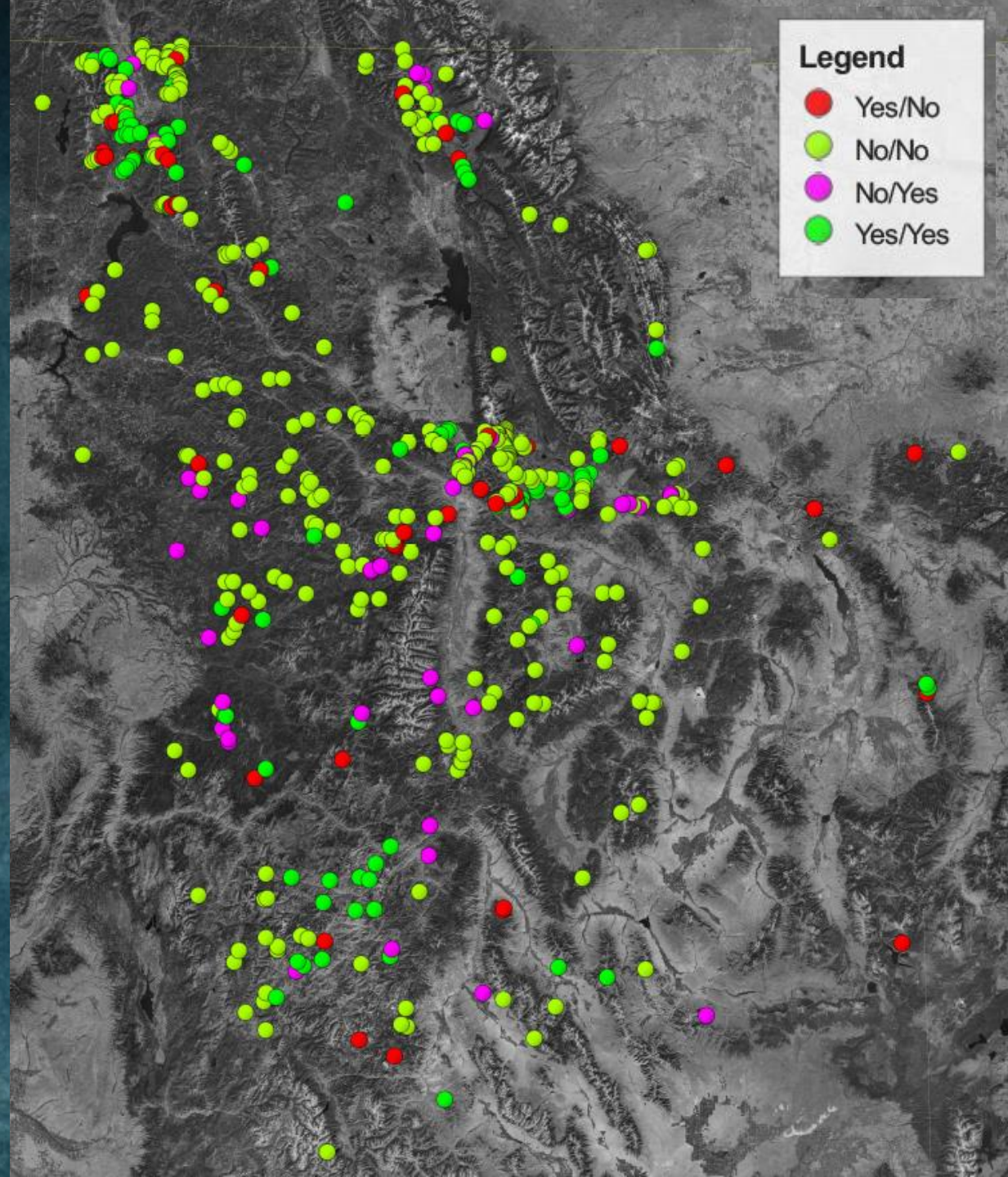
Introgression can be predicted

- Final logistic models
  - AUC ~ 0.81-0.85
  - Classification success: 71—85%

- Covariates-RT ⬆ as:
  - Temperature ⬆
  - RT range ⬆
  - Mean annual flow ⬆
  - Easting ⬆
  - Distance to RT ⬇
  - Distance to RT habitat ⬇

- Introgression can be projected
  - RT invasion incomplete
  - RT invasion has an endpoint
  - That endpoint will move
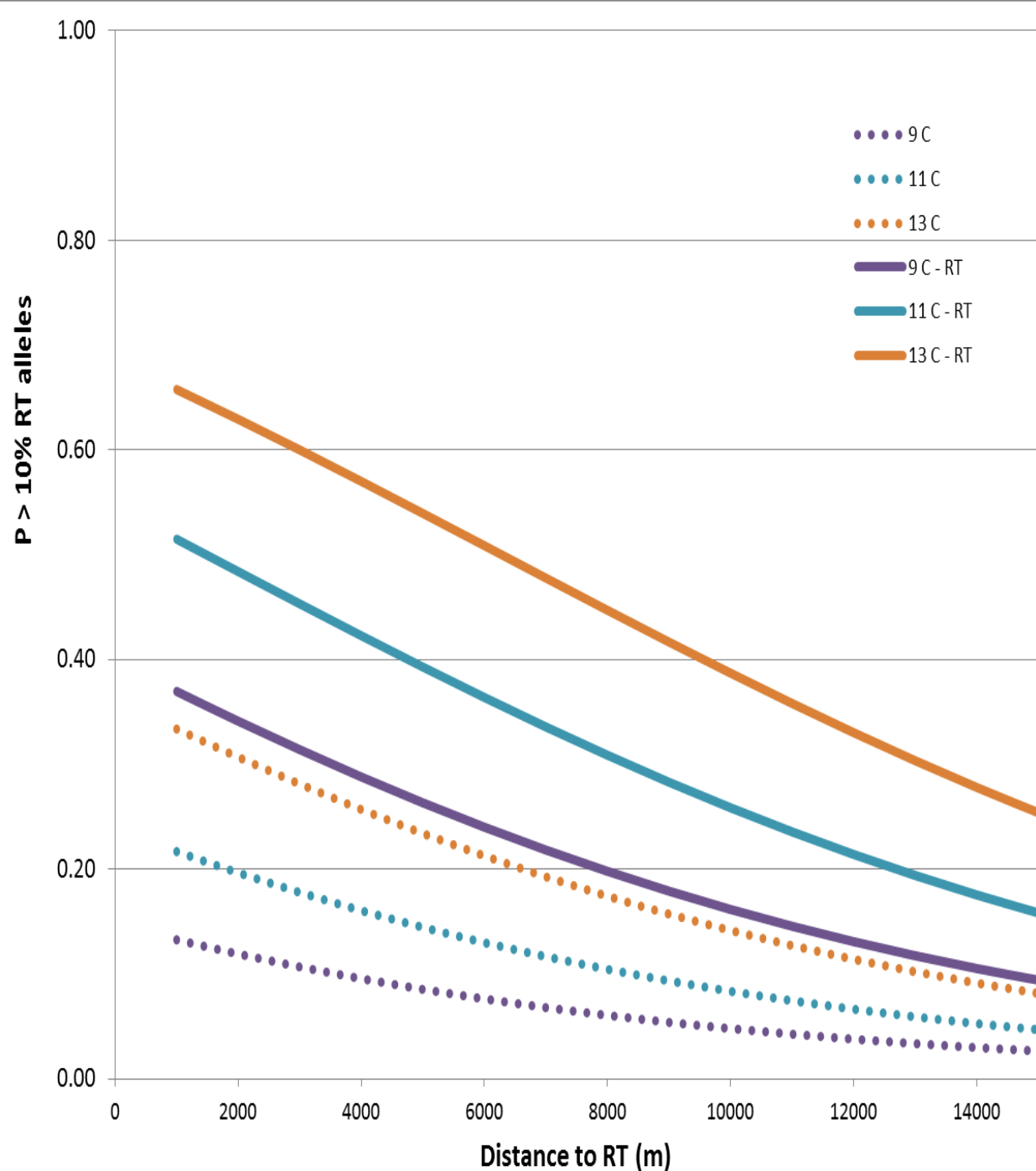
Conservation status of WCT

- Not so grim
  - 🔵 <10% WCT
  - 🟣 10–90% WCT
  - 🟪 90–99% WCT
  - 🔴 >99% WCT

- Conclusion
  - Introductions of RT are a threat

- Broad-scale, evolutionary view:
  - Hybrid swarms are a distraction
  - RT more fit where warm, large, and productive
  - Migrant WCT are at risk