

Turelli Review

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1. Speciation

BIOLOGICAL SPECIES CONCEPT: reproductively isolated e.g. [Mayr \(1942\)](#), PHYLOGENETIC SPECIES CONCEPT: need the tree, GENERAL LINEAGE CONCEPT [de Queiroz \(2005\)](#) concepts are different, somewhat arbitrary lines along a continuum of change.

1.1. Reproductive Isolating Mechanisms:

1.1.1. Prezygotic

PREZYGOTIC = mate selection, pre-mating or post-mating (cryptic).

1.1.2. Postzygotic

POSTZYGOTIC = inviable/sterile hybrids

- INTRINSIC is developmental: primary example is DOBZHANSKY-MULLER INCOMPATIBILITIES (DMIs): During allopatry, genotype may evolve in separate populations from $aabb \rightarrow AAbb$ & $aaBB$, A & B not compatible.¹
- EXTRINSIC is ecological, behavioral. Lindy [McBride](#)'s hybrid butterflies mismatch laying location on host plants, hybrid parrots can't decide to hold nest material in beak vs rump feathers.

Patterns across taxa? Oscine Birds exhibit prezygotic much sooner than postzygotic [Price et al. \(2001\)](#), [Grant & Grant \(1997\)](#), while *Drosophila* experience both at similar rates, [Coyne & Orr \(1989\)](#).

1.2. Patterns of Speciation: Active vs. Passive

Question: Is speciation primarily PASSIVE, occurring completely in allopatry without interactions, or ACTIVE, requiring REINFORCEMENT: natural selection against hybridization after secondary contact, to complete the speciation, or speciation occurring entirely in sympatry. New spin on old allopatric vs sympatric question.

1.2.1. Allopatry

- **Theory**
- **Evidence** [Jordan \(1905\)](#), [Knowlton et al. \(1993\)](#) Panama shrimp. Sister species always allopatric, i.e. *Anolis* lizards, [Losos & Schluter \(2000\)](#); islands birds, [Coyne & Price \(2000\)](#).

[Lynch \(1989\)](#) calls any range overlap sympatry. Later studies reject thoroughly, show AREA-RANGE CORRELATION (ARC plots) as evidence for allopatry, i.e. in darters [Near & Bernard \(2004\)](#). ARC later criticized, geography changes, signal not always clear, [Fitzpatrick & Turelli \(2006\)](#).

General Conclusion: Speciation driven by adaptive changes in allopatry.

1.2.2. Sympatry

- **Theory** [Dieckmann & Doebeli \(1999\)](#) Haploid model, 2-character model: ecology and assortment character linked (MAGIC TRAIT), and female preference, 3-character model: unlinked, much weaker. Sympatric speciation only when resource width broader than individual utilization width.
- **Evidence** [Walsh \(1867\)](#) apple-maggots, [Schliewen et al. \(1994\)](#) crater-lake cichlids, [Sorenson et al. \(2003\)](#) indigo birds.

un-speciation - Lake Victoria eutrophication, cichlids can't see to sexually select.

1.2.3. Reinforcement

- **Theory** Emphasizes prezygotic, since post-zygotic unlikely (though supported by Wallace originally, and requires group-selection). [Felsenstein \(1981\)](#) showed mate preference dissociates with mate preference, making reinforcement unlikely. [Slatkin \(1982\)](#) shows way out by magic trait: i.e. flowering time.
- **Evidence** [Noor \(1995\)](#) *Drosophila pseudoobscura* and *D. persimilis* show more mate choice from areas where they occur in sympatry than areas where they are in allopatry (hybrids have lower fitness). [Hoskin \(2005\)](#) Tree frogs evolve different calls where small southern species patch surrounded by northern species. Fail to do so at the north-south hybrid zone since overwhelmed by gene flow – a originally a theoretical objection called SWAMPING, [Sanderson \(1989\)](#). [Coyne & Orr \(1989\)](#) also found existing postzygotic evolution in their *Drosophila* was associated with increased prezygotic isolation for populations found in sympatry, suggesting that these postzygotic DMIs were providing the basis for prezygotic reinforcement.

1.3. Ecological Speciation

Few successful early experiments: [Dodd \(1989\)](#) *Drosophila* on different sugars, very rapid reproductive isolation, drift not responsible (replicates on same medium could still mate). [Schluter](#)'s sticklebacks natural example. [Funk et al. 2006](#) meta-analysis supports ecological divergence associated with faster pre and post-zygotic isolation.

¹ Come in many forms, including CYTOPLASMIC INCOMPATIBILITIES (*wolbachia*) or INVERSIONS.

1.4. Genetics of Speciation

Genetics of speciation are the genetics of the adaptation, few general rules. Focus on intrinsic post-zygotic evolution.

1.4.1. Haldane's Rule

heterogametic sex is the one suffering fitness loss (sterility or inviability). For sterility For inviability

1.4.2. Coyne's Rule

Also called the LARGE X EFFECT.

1.4.3. Darwin's Corollary

Effect can be asymmetric.

2. Comparative Methods

2.1. Brownian Motion and early methods

- Maddison (2000) Pruning redundant tree branches.
- Felsenstein (1985): BROWNIAN MOTION, INDEPENDENT CONTRASTS.

2.2. Markov Models

- Pagel (1994) two-parameter model.
- Maddison (2007) six-parameter model.

2.3. Niche-filling models

- Original model Price (1997) YULE-PROCESS (pure birth) model, where closest species fills the niche presented.
- Freckleton & Harvey (2006): Richer model of Price niche-filling. Also Distinguish between niche and Brownian hypotheses: (i) constant diversification rate (Brownian) vs (2) constant total rate of adding new species (iii) decelerating total rate. Look to see if node height is correlated with contrasts as evidence against Brownian motion. Empirical support Brownian in new-world warblers, niche in old world.

3. Quantitative Genetics

Study your practice problems!

3.1. Three central equations:

$$V_P = \underbrace{\text{Var}(E(P|g)_{\text{env}})_{\text{gen}}}_{V_G} + \underbrace{E(\text{Var}(P|g)_{\text{env}})_{\text{gen}}}_{V_E} \quad (1)$$

$$\text{Cov}(P_x, P_y) = 2F_{xy}\text{Var}(A) + U_{xy}\text{Var}(D) + \text{Cov}(E_x, E_y) \quad (2)$$

$$R = h^2 S \quad \text{or} \quad R = \Sigma_A \Sigma_P^{-1} S = \Sigma_A \beta \quad (3)$$

| Relationship | $F_{xy} U_{xy}$ |
|------------------|-----------------|
| Parent-Offspring | 1/4 0 |
| Full sibs | 1/4 1/4 |
| Half sibs | 1/8 0 |

Table 1

Consanguinity & the double identity coefficient for common relationships

3.2. Useful Statistics

$$(X, Y) \sim \text{BN}(\mu_X, \mu_Y, \sigma_X^2, \sigma_Y^2, \rho)$$

$$\implies P(X|Y > y) \sim 1 - \Phi\left(\frac{y - \mu}{\sigma}\right)$$

$$\text{where } \mu = \mu_X + \underbrace{\rho \frac{\sigma_X}{\sigma_Y}}_{\beta_{X|Y}} (y - \mu_Y), \quad \text{and } \sigma = \sigma_X^2 (1 - \rho^2)$$

$$\beta_{X|Y} = \frac{\text{Cov}(X, Y)}{\text{Var}(Y)}, \quad \rho = \frac{\text{Cov}(X, Y)}{\sigma_X \sigma_Y}$$

3.3. Common definitions

Two useful identities dominate quantitative genetics, and much notation is just naming parts of those identities

$$E(P) = E(\underbrace{E(P|A_{ij})_i}_{\alpha_i + \mu_P}) \quad (4)$$

$$\text{Var}(P) = \text{Var}(\underbrace{E(P|A_{ij})_{\text{env}}}_{g_{ij}})_{ij} + \underbrace{E(\text{Var}(P|A_{ij})_{\text{env}})_{ij}}_{V_E} \quad (5)$$

$$V_G = \underbrace{E(y_{ij}^2)_{ij}}_{g_{ij}}$$

A (diploid) locus has genotypes A_{ij} , i.e. AA, Aa, aa , with genotype frequencies p_{ij} . We can also consider a single allele, A_i , i.e. A or a , with allele frequencies p_i . Averaging over ij averages over genotypes, while averaging over j alone averages over all possible options for the other allele. The mean phenotype of the A_{ij} genotype is $g_{ij} = E(P|g)_{\text{env}}$. Mean over all genotypes is $\mu_P = E(g_{ij})_{\text{gen}}$, from which we get the rescaled mean phenotypes, $y_{ij} = g_{ij} - \mu_P$, while variance over genotypes is $V_G = \text{Var}(g_{ij})_{\text{gen}} = E(y_{ij}^2)_{ij}$. The additive genetic effect $\alpha_i = E(y_{ij})_j$.