Zoological Studies **65:**17 (2026)

Perspective: A Fitness Landscape Perspective on Species Boundary and Gene Flow for Taxonomic Practitioners in the Genomic Era

Jen-Pan Huang*

*Biodiversity Research Center, Academia Sinica, Nankang, Taipei 115, Taiwan. *Correspondence: E-mail: jphuang@as.edu.tw (Huang)*

(Received 2 December 2025 / Accepted 7 March 2026 / Published -- 2026)
Communicated by Chih-Ming Hung

ORCID: https://orcid.org/0000-0002-9329-8867

Speciation can be conceptualized as evolution across dynamic fitness landscapes, where groups of individuals occupy peaks or plateaus that change across space and time. Within such landscapes, gene flows between species can be expected outcomes, which result in the episodic and temporal permeability of species boundaries. Because species recognition and gene flow both arise from the same underlying fitness landscape dynamics, they are emergent, instead of causally linked, properties. Therefore, despite their frequent correlation, studies in systematics should decouple species recognition from the presence or absence of gene flow.

Keywords: Fitness landscape, Gene flow, Hybridization, Species, Systematics

Citation: Huang JP. 2026. Perspective: A fitness landscape perspective on species boundary and gene flow for taxonomic practitioners in the genomic era. Zool Stud **65:**17.

Speciation, similar to how it has long been conceptualized in population genetics, is often visualized as a journey across heterogeneous fitness landscapes, where distinct fitness peaks are separated by valleys of low fitness. This view explains why hybrids between species or locally adapted populations, assuming that fitness is the phenotype and that hybrid offspring have an intermediate genotype, tend to have reduced fitness (Fig. 1A). That is, it explains why and how we observe discontinuity between biological entities in nature. But what if this metaphor is too simplified? What if, instead of isolated peaks, different species often occupy broad plateaus of roughly equal fitness (Gavrilets 2003)? What are the ramifications of this perspective for species, gene flow, and the correlation between them? This piece aims to introduce students and practitioners of molecular taxonomy, particularly those working with genetic or genomic data, to a classic, yet less involved, perspective on how speciation occurs and is maintained, along with its implications for systematics. My goal is to offer an alternative viewpoint that helps taxonomic practitioners in the genomic era reconcile two important yet sometimes seemingly contradictory ideas. That is (1) species are discrete evolutionary entities and (2) gene flow does not undermine the species identity.

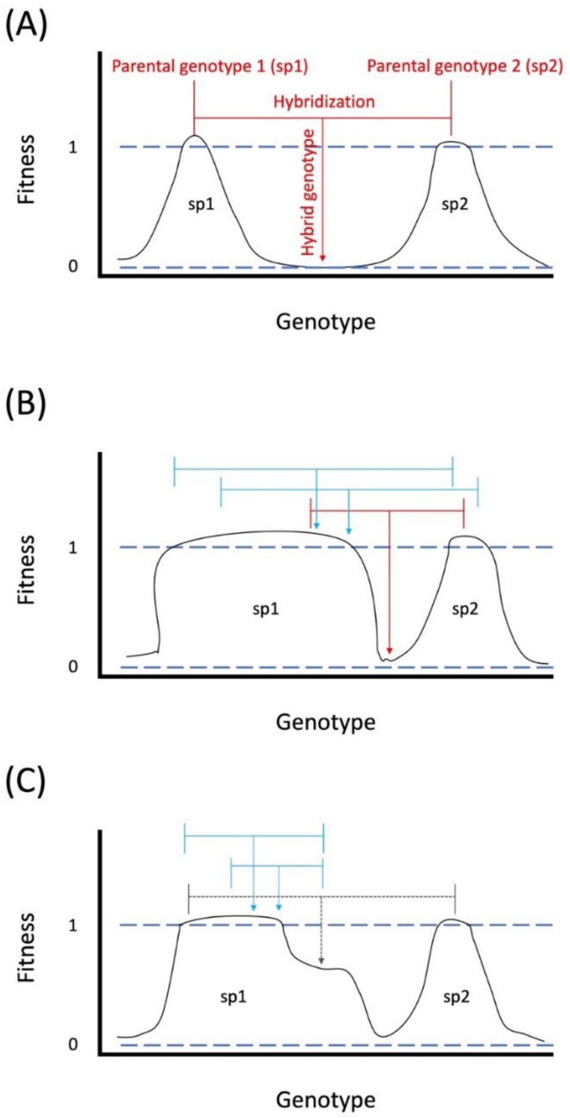

Fig. 1. A fitness landscape view of species and the outcomes of hybridization. (A) A conventional view, where hybridization between members of two species can produce unfit hybrid offspring (red lines). (B) When a species occupies a plateau of the fitness landscape, some interspecific genotype combinations may produce fit offspring (blue lines). (C) The scenarios in (A) and (B) are highly simplified. In a more realistic, though still simplified, view, some F1 hybrids may have fitness < 1 but > 0; this fitness value only indicates that the genotype may not persist under current environmental conditions (grey dashed lines) and does not imply immediate elimination (fitness = 0). Surviving F1s

may have a higher odds of producing fit (fitness ≥ 1) F2 offspring (blue lines) with parental species sp1 than with sp2. The horizontal dark blue dashed lines indicate the lower and upper fitness values of 0 and 1.

The definition of species has been a challenging concept for biologists to agree upon, especially when practitioners have different study foci or systems (Stankowski and Ravinet 2021). For example, evolutionary scientists may view species as genetic entities with independent past and future evolutionary trajectories (Maddison and Whitton 2023), whereas taxonomic practitioners may emphasize distinct phenotypes of key traits that are thought to maintain species boundaries and treat species recognition as a testable hypothesis (Brady et al. 2024). In this perspective piece, I assume that species are genetic clusters occupying discontinuous peaks and plateaus in a fitness landscape (Fig. 1). This represents a snapshot in time in which we observe evolutionarily distinct and discrete units maintained in nature. These units could be regarded as populations or local genotypes if morphological variation is insufficient to warrant species status. On the other hand, they could be treated as well-recognized species if specific local adaptation has occurred between genetic clusters or if morphological divergence is apparent (Butlin and Faria 2024).

In such a landscape (Fig. 1B), the boundaries between species may be far more permeable. Gene flow could occur as a common evolutionary process. Specifically, large plateaus could permit the immigration of foreign alleles, or gene flow, into the species, because the hybrid offspring may not always suffer fitness loss (Fig. 1B). For example, imagine there is a plateau and a peak in a one-dimensional fitness landscape, and assume again that the fitness of the hybrid is the phenotype and that the hybrid offspring will have an intermediate genotype between the parental genotypes. We can infer that hybridization between the species occupying the peak (sp2 in Fig. 2A) and the one that occupies a plateau (sp1 in Fig. 2A) will have certain odds of producing fit individuals that reside in the plateau species (sp1). As a result, directional gene flow from sp2 to sp1 is possible. However, the reverse direction of gene flow will likely always result in unfit offspring and thus is less likely to occur (Fig. 2B).

The implications of the above observations have important evolutionary and systematic implications. We often detect directional or asymmetric gene flow in nature between diverging entities, such as in our own species (*e.g.*, from Neanderthals to non-African modern humans; Green et al. 2010; Li et al. 2024). Specifically, humans occupy a large geographic range and likely a broader ecological range than those of Neanderthals. As a result, studies have commonly detected directional gene flow from Neanderthals, which likely represent a species that occupied a fitness peak, to non-African modern humans, which may represent a species that occupied a plateau on the fitness landscape.

The odds of gene flow can be impacted by the width of the valley between the peaks and plateaus (Fig. 2). Specifically, if the valley is wider than the plateaus, then hybridization between genotypes of different parental species will often result in unfit intermediate genotypes (Fig. 2C). As a result, gene flow will not be detected. Importantly, fitness landscapes are not static. Climate shifts, ecological changes, and biotic interactions can reshape their contours, expanding, contracting, or shifting these peaks and plateaus (Seehausen et al. 2014). Such fluctuations could periodically open or close channels of gene flow, implying that hybridization may not be a rare accident but rather an expected outcome of a dynamic environment. Empirically, gene flow between evolutionary entities can be periodic instead of continuous across geological time (*e.g.*, Li et al. 2024). The results probably not only represent distributional shifts in the past that likely facilitated contact and hybridization at certain points in time, but also reflect that historical changes in climatic conditions may have expanded the fitness landscape into a larger plateau, making the influx of foreign alleles more likely during certain geological periods. Viewed through this lens, speciation is not only about the divergence of different evolutionary entities by occupying different fitness peaks, but also about how they track changes in peaks and plateaus in an ever-changing terrain. Hybridization and gene flow may or may not be possible, or be detected, between species because these processes depend on the shifting fitness landscape across time and space. Additionally, along with shifts in the fitness landscape, hybridization has been argued to be a creative force for accessing novel fitness peaks that would not be possible if breeding occurred only between conspecific genotypes (Edelman and Mallet 2021; *e.g.*, Rosser et al. 2024).

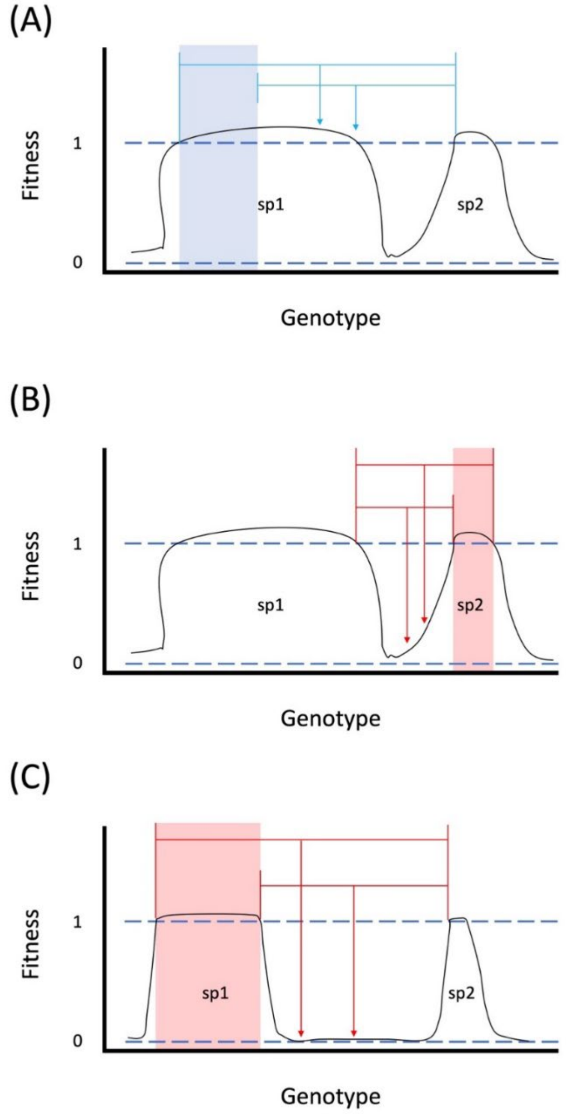

Fig. 2. A fitness landscape view of directional gene flow between species. (A) A range of genotypes in sp1 (blue shaded area), combined with the extreme left genotype of sp2, can produce fit hybrid genotypes on the plateau representing typical sp1. This process can result in directional gene flow from sp2 to sp1. (B) In contrast, none of the genotypes in sp2 (red shaded area), combined with the right-most genotype of sp1, can produce fit hybrids. Therefore, no directional gene flow is expected to occur from sp1 to sp2. (C) Following a change in environmental conditions, the relative size and shape of fitness peaks, plateaus, and valleys may change, and the valley between plateau and peak may become too wide for fit hybrid genotypes to be produced. As a result, gene flow is effectively absent, even though it existed previously from sp2 to sp1 (A). The horizontal dark blue dashed lines indicate the lower and upper fitness values of 0 and 1.

Finally, in a multidimensional fitness landscape integrating genome and genotype effects, divergent selection may turn plateaus into peaks and thus broadens valleys along specific dimensions. This process reduces hybrid fitness in those dimensions, while gene flow continues to homogenize most others (cf. Wu 2001). Over time, reproductive isolation can be achieved when the landscape only forms narrow fitness peaks with broad and deep valleys in between the peaks. Specifically, the valleys between peaks may become so wide, gradually or suddenly depending on the pace of environmental change, that future shifts can no longer generate fit hybrids. This point of no return, or tipping point (Nosil et al. 2017), may mark the completion of speciation. Nevertheless, detecting this tipping point remains challenging.

The ramifications on species, gene flow, and their correlation

The number of species are thus emergent properties of the ever changing fitness landscape determined by the number of peaks and plateaus at the time and place of investigation. Furthermore, the existence, direction, and strength of gene flow is also an emergent property of this ever changing landscape determined by the relative width of the valley and the expand of the plateaus (Fig. 2). Therefore, the support, or detection, of gene flow may not be generalized to argue for or against biological species recognition, even though the two may be highly correlated because of shared determination factors. For example, does geographically isolated entities without gene flow equates species? Or does gene flow between different locally adaptive forms is a sign of intraspecific relationship between the studied groups? Many empirical studies will argue against these claims as the predictions are largely determined by historical contingencies (Baum & Shaw; 1995; Maddison & Whitton 2023). The delineation between species and population may often be determined by the regional or system specific culture of where to draw the line (Huang & Knowles 2016; Stankowski & Ravinet 2021). It is never as simple as to test whether two different entities can produce viable and fertile offspring (Wilson & Brown 1953), because a species is a population and one could never know how many different pairs of interbreeding experiments are needed to say for sure that members from the two tested species could never produce viable progenies (Figs. 1 & 2). The only thing that are statistically testable and experimental tractable is whether gene flow and/or hybridization occurred between the two focal species. And even if the result is a resounding yes, it still does not warrant an intra-specific relationship (Baum & Shaw 1995; Wu 2001; Seehausen et al. 2014; Edelman & Mallet 2021).

Whether or should the evolutionary entities that are still in the same ever changing fitness landscape represent different species would be a different and challenging question to answer. Specifically, one naïve assumption of this simplified perspective is that different genotypes can freely encounter and recombine with one another. Of course, this is not always the case in empirical systems. For example, the evolution of lock-and-key mating structures or the presence of physical, unsurpassable barriers can reduce, or even completely preclude, the opportunity for recombination between certain genotypes (Mayr 1963; Shapiro & Porter 1989). Additionally, when there is an important regime shift in how the genomic network integrating different elements to produce fit phenotypes, then most of the time practitioners will have no issues calling these entities as different species (such as the whole genome epistatic evolution, or the snow ball effect; Mayr 1963; Orr 1995; Nosil et al. 2017). However, this regime change may not often occur between what have been recognized as good species by taxonomists (Huang 2020; Kulmuni et al. 2020). What we name today as different species versus populations are often only separate by the magnitudes of the relative width of the valleys and the size of the plateaus in the fitness landscape (Figs. 1 & 2). Keep in mind that this landscape is changing all the time, so the dynamics between defining populations versus species may also have to be changed all the time. Biological species are real, because we see independent entities and discontinuities in genetics and phenotypes in nature; however, some of the discontinuity and independence can be evolutionarily ephemeral, while others transcendent. More importantly, whether a species today will become transcendent depends on changes in the fitness landscape, instead of on the presence of gene flow, which has often been the presumed homogenizing force.

Incompatibility between genotypes or between species?

Interestingly, the classical model of allopatric speciation and evo-devo share similar genomic perspectives for understanding the mechanisms through which incompatibility arises. The idea of the evolution of epistatic interactions in the genome between isolated species described by Mayr (1963) is conceptually, and perhaps surprisingly, similar to what has been hypothesized as developmental system drift (True & Haag 2001) in evo-devo studies. The mechanism describes how similar phenotypes can be maintained despite extensive underlying genetic divergence. Because developmental and regulatory networks are highly epistatic, compensatory changes can accumulate while buffering phenotypic output. When such changes are recombined in hybrids, mismatched components may disrupt developmental stability and result in incompatibilities. Such incompatibilities, nevertheless, can also evolve within species (Corbett-Detig et al. 2013), which also indicates that there is no definitive association between species recognition and incompatibility. If the "point of no return," where different genotypes can no longer produce compatible hybrids, is the focus of your study, then, the question might be less about what species are or how they came to be; instead, it concerns more specifically how genetic networks or epistatic interactions between genes in the genome evolve.

The implications of such studies are undoubtedly relevant to speciation and reproductive isolation, especially in the genomic era. However, they represent only one of many possible mechanisms, or stages (Kulmuni et al. 2020), that may explain why we observe discontinuities among evolutionary units in nature. What I would like to emphasize here is that incompatibility tests are typically conducted between individual organisms or among individuals carrying different genotypes, and thus the outcomes reflect genotype–genotype interactions rather than species-level properties. A species, however, is composed of a diverse pool of genotypes. As a result, incompatibility and species recognition should be conceptually decoupled; *i.e.*, incompatibilities detected between particular genotypes do not constitute direct evidence about the boundaries or reality of species as evolutionary units, nor are they causal determinants of species status. Thus, incompatibility and species recognition operate at different biological levels and should not be conflated.

Acknowledgments: I would like to thank Academia Sinica for an internal research support and the National Science and Technology Council of Taiwan for research funding (114-2621-B-001-006-MY3). I thank the reviewer for providing very thoughtful and insightful comments that helped improve the clarity and broaden the general interest of the manuscript.

Authors' contributions: JPH conducted all aspects of this work.

Competing interests: None declared.

Availability of data and materials: JPH declares no conflict of interest.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Baum DA, Shaw KL. 1995. Genealogical perspectives on the species problem. Experimental and Molecular Approaches to Plant Biosystematics **53:**289–303.

Brady MF, Hsu Y-F, Lamas G. 2024. How to describe a new species in zoology and avoid mistakes. Zool J Linn Soc **202:**zlae043. doi:10.1093/zoolinnean/zlae043.

Butlin RK, Faria R. 2024. Local adaptation and reproductive isolation: when does speciation start? Evol J Linn Soc **3:**kzae003. doi:10.1093/evolinnean/kzae003.

Corbett-Detig RB, Zhou J, Clark AG, Hartl DL, Ayroles JF. 2013. Genetic incompatibilities are widespread within species. Nature **504:**136–137. doi:10.1038/nature12678.

Edelman NB, Malles J. 2021. Prevalence and adaptive impact of introgression. Annu Rev Genet **55:**265–283. doi:10.1146/annurev-genet-021821-020805.

Gavrilets S. 2003. Perspective: models of speciation: what have we learned in 40 years. Evolution **57:**2197–2215. doi:10.1111/j.0014-3820.2003.tb00233.x.

Green RE, Krause J, Briggs AW et al. 2010. A draft sequence of the Neandertal Genome. Science **328:**710–722. doi:10.1126/science.1188021.

Huang J-P, Knowles LL. 2016. The species versus subspecies conundrum: quantitative delimitation from integrating multiple data types within a single Bayesian approach in Hercules beetles. Zool Syst **65:**685–699. doi:10.1093/sysbio/syv119.

Huang J-P. 2020. Is population subdivision different from speciation? From phylogeography to species delimitation. Ecol Evol **10:**6890–6896. doi:10.1002/ece3.6524.

Kulmuni J, Butlin RK, Lucek K, Savolainen V, and Westram AM. 2020. Towards the completion of speciation: the evolution of reproductive isolation beyond the first barriers. Philos Trans R Soc Lond **B** Biol Sci **375:**20190528. doi:10.1098/rstb.2019.0528.

Li L, Comi TJ, Bierman RF, and Akey JM. 2024. Recurrent gene flow between Neanderthals and modern humans over the past 200,000 years. Science **385:**eadi768. doi:10.1126/science.adi1768.

Maddison W, Whitton J. 2023. The species as a reproductive community emerging from the past. Bulletin of the Society of Systematic Biologist **2:**135. doi:10.18061/bssb.v2i1.9358.

Mayr E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, MA.

Nosil P, Feder JL, Flaxman SM, and Gompert Z. 2017. Tipping points in the dynamics of speciation. Nat Ecol Evol **1:**0001. doi:10.1038/s41559-016-0001.

Orr HA. 1995. The population genetics of speciation: the evolution of hybrid incompatibility. Genetics **139:**1805–1813. doi:10.1093/genetics/139.4.1805.

Rosser N, Seixas F, Queste LM et al. 2024 Hybrid speciation driven by multilocus introgression of ecological traits. Nature **628:**811–817. doi:10.1038/s41586-024-07263-w.

Seehausen O, Rutlin RK, Keller I et al. 2014. Genomics and the origin of species. Nat Rev Genet **15:**176–192. doi:10.1038/nrg3644.

Shapiro AM, Porter AH. 1989. The lock-and-key hypothesis: evolutionary and biosystematics interpretation of insect genitalia. Annu Rev Entomol **34:**231–245. doi:10.1146/annurev.en.34.010189.001311.

Stankowski S, Ravinet M. 2021. Quantifying the use of species concept. Current Biology **31:**PR428–R429. doi:10.1016/j.cub.2021.03.060

True JR, Haag ES. 2001. Developmental system drift and flexibility in evolutionary trajectories. Evol Dev **3:**109–119. doi:10.1046/j.1525-142x.2001.003002109.x.

Wilson EO, Brown Jr. WL. 1953. The subspecies concept and its taxonomic application. Syst Biol **2:**97–111. doi:10.2307/2411818.

Wu C-I. 2001. The genic view of the process of speciation. Journal of Evolutionary Biology **14:**851–865. doi:10.1046/j.1420-9101.2001.00335.x.