A flexible method for estimating tip diversification rates across a range of speciation and extinction scenarios

Supplementary Material 7

Short terminology survey on "turnover rates"

Readers may wonder about our usage of "turnover" (τ) as a parameter describing the speciation rate + extinction rate. Turnover is commonly used in the paleontology literature as speciation (or origination) + extinction (examples in Table SM6.1), but less so in the neontological literature (examples in Table SM6.2) where it is often used as extinction/speciation (examples in Table SM6.3). However, we emphasize its usage as speciation + extinction here (as the examples in Table SM6.2) because we believe that many diversification hypotheses may be better described by turnover rates rather than net-diversification (e.g. our empirical example). Also note that, because the R package *hisse* (which includes all MiSSE related functions) has been using turnover rates as speciation + extinction for almost five years (Caetano et al. 2018), users of this package have already gotten accustomed to this notation (examples in Table SM6.4). This also contributed to our reasoning that it would not be parsimonious to change the terminology now, even though the usage of this term in the literature is not always consistent.

We also note that, in our usage, turnover is a rate with units as events per unit of time, whereas turnover as extinction/speciation (which we call extinction-fraction) is a proportion rather than a rate. Turnover as a rate makes sense when rates of extinction approach those of speciation, which we assume to be true in most natural systems (even when current models do not always do a good job in capturing it). Of course, turnover rates only make sense when extinction is different from 0, since turnover rates collapse into speciation rates when extinction is 0 and thus turnover *per se* does not occur. This is probably the reason why this notation is more commonly used in the paleontological literature where extinction events are more straightforward to measure (even when the fundamental process being measured is the same).

Table SM6.1: Turnover as speciation (or origination) + extinction in the paleontology literature.

What's been described	Reference	DOI	Term used	Example of usage
speciation + extinction + migration	Vrba 1993	10.2475/ajs.293.A.418	lineage turnover	"For the discussion that follows I remind the reader that my use of the term **lineage turnover** includes speciation, extinction, and migration, all of which change the composition of species in particular areas"
speciation + extinction / diversity	Lasker 1978	10.1017/S0094837300005819	turnover rates	"At each time unit a new taxon is added to the record. Low diversity at the start of the record leads to an extremely high **turnover rate** which very rapidly declines as the total diversity increases."
speciation + extinction	Wei & Kennett 1986	10.1029/PA001i001p00067	rate of turnover	"In order to indicate the total change in assemblages, we followed Lasker (1978) to define the **rate of turnover** as rt=rs+re"
	Leckie et al. 2002	10.1029/2001PA000623	rate of turnover	"rate of extinction ((1/S)LO); rd, rate of diversification (rs − re); rt, **rate of turnover** (rs + re). "
	van Dam et al. 2006	10.1038/nature05163	turnover rate	See Figure 1. in the original paper.
	Kiessling & Aberhan 2007	10.1666/06069.1	turnover rates	"Extinction (E) and origination (O) rates are reported as per-genus rates following Foote (2000, 2003). **Turnover rates** (E + O) and diversification rates (O − E) were also computed. "
	Xing et al. 2014	10.1111/evo.12489	turnover rates	See Figure 4 in the original paper. "Figure 4: The three epochs with high **turnover rates** are shaded orange and coincide with severe global climate change, the epochs with low **turnover rates** are shaded green."
	Crampton et al. 2016	10.1073/pnas.1600318113	species turnover and turnover rate	"We identify five major episodes of **species turnover** (origination rate plus extinction rate) that were coincident with times of cooling in southern high-latitude climate, Antarctic ice sheet growth across the continental shelves, and

				associated seasonal sea-ice expansion across the Southern Ocean."
Crampton et al. 2018	10.1073/pnas.1714342115	turnover probability		"Here, we show that, relatively early in the history of complex life, Milankovitch "grand cycles" associated with astronomical rhythms explain between 9 and 16% of variation in species **turnover probability**(extinction probability plus speciation probability) in a major Early Paleozoic zooplankton group, the graptoloids"

Table SM6.2: Turnover as speciation + extinction in the neontological literature.

What's been described	Reference	DOI	Term used	Example of usage
speciation + extinction	Weir & Schluter 2007	10.1126/science.1135590	rate of species turnover	"Despite these uncertainties, our results suggest that elevated speciation and extinction rates in the temperate zone can drive high turnover of species, whereas **rates of species turnover** at tropical latitudes are reduced"
	Sidlauskas 2007	10.1111/j.1558-5646.2007.00022.x	lineage turnover and turnover rate	"Second, variation in the historical rate of **lineage turnover** (combined speciation and extinction rates) can produce unequal morphological diversities. An increase in **turnover rates**concentrates nodes connecting surviving species near the modern time horizon"
	Ribera et al. 2008	10.1046/j.1365-294x.2001.01218.x	turnover and species turnover	"Levels of **turnover** between the two clades can be distinguished by the absolute values of b and d, which will be higher in the clade with the highest **species turnover** (even if the difference b – d has the same value in both)"
	Antonelli et al. 2015	10.3389/fgene.2015.00130	species turnover	"The outstanding species richness of angiosperms found today in the Neotropics as compared to tropical Africa and tropical Asia is associated with significantly higher speciation and extinction rates in the Neotropics (Figures 6C,D)—and

				thereby higher **species turnover** and shorter average longevity of species."
Chevin 2016	10.1111/evo.12879	turnover rate		"The analysis reveals that both the net diversification rate (speciation − extinction) and the **turnover rate**(speciation + extinction) are important for the expected and random part of macroevolution"
Cutter & Gray 2016	10.1111/evo.13030	species turnover		"Consequently, we expect high latitudes to exhibit greater **species turnover** because they experience both faster speciation and a higher effective extinction rate than in the tropics […] "

Table SM6.3: Turnover as extinction/speciation. * note that extinction/speciation is not a rate

What's been described	Reference	DOI	Term used	Example of usage
extinction / speciation	Alfaro et al. 2009	10.1073/pnas.0811087106	turnover	"First, the background tempo of diversification for large sections of the gnathostome tree of life is characterized by a low overall net rate (r 0.010 lineages/Myr) but also high **turnover** where the death rate is 99% of the birth rate (Fig. 1)."
	Stadler 2012	10.1093/sysbio/sys073	turnover	"I conclude that for high **turnover** μ/λ, it is very important to condition on survival."
	Stadler 2013	10.1111/jeb.12139	turnover	"The above methods attempt to estimate speciation and extinction rates as well as their changes. It has been widely recognized that although diversification (= speciation − extinction) can be calculated with high confidence, the **turnover**(extinction/speciation) is very hard to estimate"
	Kergoat et al. 2014	10.1186/s12862-014-0220-1	turnover	"The period when diversification (=speciation - extinction) and **turnovers**(=extinction/speciation) changed was inferred to have been the boundary between the Early and Late Cretaceous in the middle of the KTR (shift time at ca. 103 Ma for the best-fit calibration procedure; Figure 3a, Table 1"
	Alroy 2015	10.1017/pab.2015.26	turnover rate *	"Finally, varying the**turnover rate** between 0 and 1 while holding ps

	Reference	DOI	Term used	Example of usage
				to 0.3 demonstrates that the correction is helpful even at relatively good sampling levels of around ps=0.5 (Fig. 4A)."
	Betancur-R et al. 2015	10.1111/ele.12423	turnover rate *	"We implemented models that account for state dependent diversification (SSE) to assess whether net diversification (speciation – extinction) and **turnover**(extinction/speciation) rates differ among marine and freshwater clades (prediction 2)"
	Hagen et al. 2015	10.1093/sysbio/syv001	turnover	"However, higher γ values were obtained for increased **turnover**(extinction rate divided by speciation rate), as expected under the pull-of-the-present effect (Nee et al. 1994). "
	Maliet et al. 2019	10.1038/s41559-019-0908-0	turnover and turnover rate *	"Homogeneous across all lineages in the clade ($\mu_i = \mu_0$ for all lineages, ClaDS1) or vary across lineages, but with a constant **turnover** (i.e. mu/lambda" "This is true even when simulations and inferences are performed under simple models with constant extinction or **turnover rate**."
	Warnock et al. 2020	10.1017/pab.2020.12	turnover	"We simulated three sets of trees (each 100 replicates) conditioning on extant tips n = 100 with three different levels of **turnover** (r = μ/λ)—low (r = 0.1), medium (r = 0.5), and high (r = 0.9)"
	Meseguer et al. 2020	10.1111/geb.13141	turnover	"Bayesian posterior distributions for net diversification (r = speciation minus extinction), **turnover** (a = extinction/speciation) and dispersal rates"

Table SM6.4: Mentions of speciation + extinction as turnover or turnover rate by users of the R package *hisse*.

What's been described	Reference	DOI	Term used	Example of usage
speciation + extinction	Roman-Palacios et al. 2020	10.1098/rspb.2020.0962	turnover rate	"Based on the best-fitting model, we found similar rates of diversification (figure 2; mean diversification rate polyploids = 0.199 events Myr−1, diploids = 0.217 events Myr−1; electronic supplementary material, table S4) and turnover for polyploids and diploids (mean turnover rate

			polyploids = 1.927 events Myr−1, diploids = 1.214 events Myr−1). "
Burridge & Waters 2020	10.1111/evo.14066	turnover	"The parameters of the HiSSE model are rates of transition among character states (diadromy, hidden state: presence/absence), and species turnover (speciation + extinction) and extinction fraction (extinction/speciation). "
Laenen et al. 2016	10.1111/nph.13835	turnover	"We tested 22 competing models, from the null models to the complete HiSSE model. These 22 models implemented identical transition rates (q) among states of the observed and hidden character, respectively, but exhibited increasing levels of complexity depending on **whether turnover rates** (tau), extinction fraction (eps), or the combination thereof, were allowed to vary between unisexual and bisexual lineages.
Désamoré et al. 2020	10.1111/mec.14492	turnover	The corollary is that lotic species with smaller geographical range and a higher probability of allopatric speciation would have higher species turnover over time than lentic species. Lotic lineages are expected to have a higher speciation rate (λ) and a higher extinction rate (μ), with the consequence that turnover ($\lambda + \mu$) is expected to be higher, but not necessarily net diversification rates ($\lambda - \mu$).
Padilla-Morales et al. 2021	10.1111/een.13115	net-turnover	See Table 1 in original publication.
Brock et al. 2021	10.1093/sysbio/syab046	net-turnover	See Table 2 in original publication.
Miller and Wiens 2017	10.1111/ele.12783	turnover	HiSSE optimises species turnover ($\tau = \lambda + \mu$) and the extinction fraction ($\varepsilon = \mu/\lambda$) for states 1A, 1B, 0A and 0B, where 1 and 0 represent habitat and A and B, the hidden states.

References

Alfaro, M. E., Santini, F., Brock, C. D., Alamillo, H., Dornburg, A., et al. (2009). Lineage-specific diversification rates and high turnover in the history of jawed vertebrates. *Proc Natl Acad Sci USA*, *106*(32), 13410-13414.

Alroy, J. (2015). A more precise speciation and extinction rate estimator. *Paleobiology*, *41*(4), 633-639.

Antonelli, A., Zizka, A., Silvestro, D., Scharn, R., Cascales-Miñana, B., & Bacon, C. D. (2015). An engine for global plant diversity: highest evolutionary turnover and emigration in the American tropics. *Frontiers in Genetics*, *6*, 130.

Betancur-R, R., Ortí, G., & Pyron, R. A. (2015). Fossil-based comparative analyses reveal ancient marine ancestry erased by extinction in ray-finned fishes. *Ecology Letters*, *18*(5), 441-450.

Brock, K. M., McTavish, E. J., & Edwards, D. L. (2022). Color polymorphism is a driver of diversification in the lizard family Lacertidae. *Systematic Biology*, *71*(1), 24-39.

Burridge, C. P., & Waters, J. M. (2020). Does migration promote or inhibit diversification? A case study involving the dominant radiation of temperate Southern Hemisphere freshwater fishes. *Evolution*, *74*(9), 1954-1965.

Chevin, L. M. (2016). Species selection and random drift in macroevolution. *Evolution*, *70*(3), 513-525.

Crampton, J. S., Cody, R. D., Levy, R., Harwood, D., McKay, R., & Naish, T. R. (2016). Southern Ocean phytoplankton turnover in response to stepwise Antarctic cooling over the past 15 million years. *Proceedings of the National Academy of Sciences*, *113*(25), 6868-6873.

Crampton, J. S., Meyers, S. R., Cooper, R. A., Sadler, P. M., Foote, M., & Harte, D. (2018). Pacing of Paleozoic macroevolutionary rates by Milankovitch grand cycles. *Proceedings of the National Academy of Sciences*, *115*(22), 5686-5691.

Cutter, A. D., & Gray, J. C. (2016). Ephemeral ecological speciation and the latitudinal biodiversity gradient. *Evolution*, *70*(10), 2171-2185.

Dam, J. V., Aziz, H. A., Álvarez-Sierra, M., Hilgen, F. K., & Hoek Ostende, L. W. van den, Lourens, LJ, Mein, P. Van, Meulen, AJ van der & Peláez-Campomanes. *Long-period astronomical forcing of mammal turnover. Nature*, *443*, 687-691.

Désamoré, A., Laenen, B., Miller, K. B., & Bergsten, J. (2018). Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae). *Molecular Ecology*, *27*(4), 979-993.

Hagen, O., Hartmann, K., Steel, M., & Stadler, T. (2015). Age-dependent speciation can explain the shape of empirical phylogenies. *Systematic biology*, *64*(3), 432-440.

Kergoat, G. J., Bouchard, P., Clamens, A. L., Abbate, J. L., Jourdan, H., et al. (2014). Cretaceous environmental changes led to high extinction rates in a hyperdiverse beetle family. *BMC evolutionary biology*, *14*(1), 1-13.

Kiessling, W., & Aberhan, M. (2007). Environmental determinants of marine benthic biodiversity dynamics through Triassic–Jurassic time. *Paleobiology*, *33*(3), 414-434.

Laenen, B., Machac, A., Gradstein, S. R., Shaw, B., Patiño, J., et al. (2016). Increased diversification rates follow shifts to bisexuality in liverworts. *New Phytologist, 210*(3), 1121-1129.

Lasker, H. R. (1978). The measurement of taxonomic evolution: preservational consequences. *Paleobiology*, *4*(2), 135-149.

Leckie, R. M., Bralower, T. J., & Cashman, R. (2002). Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous. *Paleoceanography*, *17*(3), 13-1.

Maliet, O., Hartig, F., & Morlon, H. (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature ecology & evolution*, *3*(7), 1086-1092.

Meseguer, A. S., Antoine, P. O., Fouquet, A., Delsuc, F., & Condamine, F. L. (2020). The role of the Neotropics as a source of world tetrapod biodiversity. *Global Ecology and Biogeography*, *29*(9), 1565-1578.

Miller, E. C., & Wiens, J. J. (2017). Extinction and time help drive the marine-terrestrial biodiversity gradient: is the ocean a deathtrap?. *Ecology letters*, *20*(7), 911-921.

Padilla-Morales, B., Cornejo-Páramo, P., García-Miranda, O., Carrillo Muñoz, A. I., Nieto López, A., et al. (2021). Fast species diversification among dragonflies (Anisoptera: Odonata: Insecta) inhabiting lentic environments regardless of wing pigmentation. *Ecological Entomology*.

Ribera, I., Barraclough, T. G., & Vogler, A. P. (2001). The effect of habitat type on speciation rates and range movements in aquatic beetles: inferences from species-level phylogenies. *Molecular Ecology*, *10*(3), 721-735.

Román-Palacios, C., Molina-Henao, Y. F., & Barker, M. S. (2020). Polyploids increase overall diversity despite higher turnover than diploids in the Brassicaceae. *Proceedings of the Royal Society B*, *287*(1934), 20200962.

Sidlauskas, B. (2007). Testing for unequal rates of morphological diversification in the absence of a detailed phylogeny: a case study from characiform fishes. *Evolution*, *61*(2), 299-316.

Stadler, T. (2013). How can we improve accuracy of macroevolutionary rate estimates?. *Systematic biology*, *62*(2), 321-329.

Stadler, T. (2013). Recovering speciation and extinction dynamics based on phylogenies. *Journal of evolutionary biology*, *26*(6), 1203-1219.

Vrba, E. S. (1993). Turnover-pulses, the Red Queen, and related topics. *American Journal of Science*, *293*(A), 418.

Warnock, R. C., Heath, T. A., & Stadler, T. (2020). Assessing the impact of incomplete species sampling on estimates of speciation and extinction rates. *Paleobiology*, *46*(2), 137-157.

Wei, K. Y., & Kennett, J. P. (1986). Taxonomic evolution of Neogene planktonic foraminifera and paleoceanographic relations. *Paleoceanography*, *1*(1), 67-84.

Weir, J. T., & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, *315*(5818), 1574-1576.

Xing, Y., Onstein, R. E., Carter, R. J., Stadler, T., & Peter Linder, H. (2014). Fossils and a large molecular phylogeny show that the evolution of species richness, generic diversity, and turnover rates are disconnected. *Evolution*, *68*(10), 2821-2832.