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Appendix B. Derivation of the occupancy distributions, matching/mismatching components, and average Jaccard turnover index for communities that minimize and maximize species turnover.

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Definitions

α_i = alpha diversity or species richness of the ith quadrat, a non-zero integer

$\bar{\alpha}$ = mean species richness of the 4 quadrats, a real non-zero number, when the assumption of constant richness is imposed, this is a positive integer.

$4\bar{\alpha}$ = total number of "occupancy units" or filled cells in the species-by-site matrix.

γ = gamma diversity or total unique species summed over all 4 quadrats, a positive integer.

x_i = number of species occurring in i quadrats where i = 1, 2, 3 or 4. This quantity is referred to as the occupancy level.

$\mathbf{x} = [x_1, x_2, x_3, x_4]$ = the occupancy frequency distribution, each element of this vector represents the number of species at a given occupancy level.

a = the number of shared species in a single pairwise comparison between quadrats, an integer (*a* in Legendre and Legendre 1998, p254). Although a is not a constant, we represented it as a non-italicized symbol for visual clarity in our expressions. In the text, **a** represents the vector of a values.

b = c = $\bar{\alpha}$ – a = the number of unique species in a single quadrat resulting from a pairwise comparison with another quadrat, an integer (*b* and *c* in Legendre and Legendre 1998, p254). The number of unique species in each quadrat is equal under the constraint that $\alpha_i = \bar{\alpha}$.

$\bar{T}_J = (1/6)\sum_{k=1}^{6}\left[2(\bar{\alpha}-\mathrm{a}_k)/(2\bar{\alpha}-\mathrm{a}_k)\right]$ = average turnover as defined by the Jaccard index of dissimilarity when $\alpha_i = \bar{\alpha}$; a_k is the number of shared species in the kth unique pairwise comparison in the system of four quadrats, a real number between 0 and 1.

$z = \log_2(\gamma/\bar{\alpha})/2$ = slope of the species-area relationship for a system of four equal area quadrats, a real number between 0 and 1.

Bold lowercase letters represent vectors throughout this treatment.

System equations

$$x_1 + x_2 + x_3 + x_4 = \gamma \qquad \text{(B.1)}$$

$$x_1 + 2x_2 + 3x_3 + 4x_4 = 4\bar{\alpha} \qquad \text{(B.2)}$$

$$\bar{\alpha} \le \gamma \le 4\bar{\alpha} \qquad \text{(B.3)}$$

Summary of findings

Table B1. The equations that define occupancy, average turnover, and the matching/mismatching components as a function of $\bar{\alpha}$ and γ. Note that in our framework b = c.

	constraints	$\mathbf{x} = [x_1, x_2, x_3, x_4]$	$\bar{T}_J$ *	a*	b, c*
Minimum $\bar{T}_J$					
	$x_{4max} - x_{4int} = 0$	$[\gamma - x_{4max}, 0, 0, x_{4max}]$	$2(\bar{\alpha} - x_{4max}) / (2\bar{\alpha} - x_{4max})$	x_{4max}	$\bar{\alpha} - x_{4max}$
	$x_{4max} - x_{4int} = 1/3$	$[\gamma - x_{4int} - 1, 1, 0, x_{4int}]$	$(1/6)\cdot\{2(\bar{\alpha} - x_{4int} - 1) / (2\bar{\alpha} - x_{4int} - 1) + 5[2(\bar{\alpha} - x_{4int}) / (2\bar{\alpha} - x_{4int})]\}$	$x_{4int} + 1$ OR x_{4int}	$\bar{\alpha} - x_{4int} - 1$ OR $\bar{\alpha} - x_{4int}$
	$x_{4max} - x_{4int} = 2/3$	$[\gamma - x_{4int} - 1, 0, 1, x_{4int}]$	$(1/2)\cdot[2(\bar{\alpha} - x_{4int} - 1) / (2\bar{\alpha} - x_{4int} - 1) + 2(\bar{\alpha} - x_{4int}) / (2\bar{\alpha} - x_{4int})]$	$x_{4int} + 1$ OR x_{4int}	$\bar{\alpha} - x_{4int} - 1$ OR $\bar{\alpha} - x_{4int}$
Maximum $\bar{T}_J$					
	$4\bar{\alpha}/2 \le \gamma \le 4\bar{\alpha}$	$[2\gamma - 4\bar{\alpha}, 4\bar{\alpha} - \gamma, 0, 0]$	$(2\bar{\alpha} + \gamma) / (4\bar{\alpha} + \gamma/2)$	$2\bar{\alpha}/3 - \gamma/6$	$\bar{\alpha}/3 + \gamma/6$
	$4\bar{\alpha}/3 \le \gamma < 4\bar{\alpha}/2$	$[0, 3\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 2\gamma, 0]$	$(\gamma - 2\bar{\alpha}/3) / (\gamma/2 + 2\bar{\alpha}/3)$	$4\bar{\alpha}/3 - \gamma/2$	$\gamma/2 - \bar{\alpha}/3$
	$\bar{\alpha} \le \gamma < 4\bar{\alpha}/3$	$[0, 0, 4\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 3\gamma]$	$2(\gamma - \bar{\alpha}) / \gamma$	$2\bar{\alpha} - \gamma$	$\gamma - \bar{\alpha}$

* When maximizing $\bar{T}_J$, the formulas in these columns are not applicable unless the formula for the matching component, a, yields an integer.

Table B2. Average turnover as a function of the slope of the species-area relationship, *z* (this is Table 1 in the main text).

	Domain of *z*	$\bar{T}_J$
Minimize $\bar{T}_J$		
	$[0,1]$	$(2^{2z} - 1)/(2^{2z-1} + 1)$
Maximize $\bar{T}_J$		
	$[0.5,1]$	$(2^{2z-1} + 1)/(2^{2z-2} + 2)$
	$[\log_2(4/3)/2, 0.5)$	$(2^{2z} - \frac{2}{3})/(2^{2z-1} + \frac{2}{3})$
	$[0, \log_2(4/3)/2)$	$2 - 2^{1-2z}$

In the following treatment, there are two primary sections which approach the respective problems of minimizing and maximizing average turnover. In both of these two sections, we will first define the occupancy distributions (**x**), and then we will define average turnover under the additional assumption of constant richness. We will provide the matching/mismatching components (a, b, and c) that Legendre and Legendre (1998, p254) have used to mathematically express many different turnover indices for presence-absence data. Lastly in both sections, we derive an expression of average turnover as a function of the slope of the species-area relationship (*z*).

1 - **Minimizing Pairwise Turnover**

1.1 - Occupancy distributions that minimize turnover for a given $\bar{\alpha}$ and γ

Turnover will be lowest when the number of species with maximal occupancy is greatest (i.e., when x_4 is maximized). If we imagine assigning x_4 species to that maximal level of occupancy, then the number of occupancy units remaining to be assigned to x_1, x_2, and x_3 must be at least as great as the number of species remaining to be assigned:

$$4\bar{\alpha} - 4x_4 \geq \gamma - x_4. \tag{B.4}$$

Rewritten, the maximal value of x_4 must satisfy the equation

$$x_4 \leq (4\bar{\alpha} - \gamma)/3 \tag{B.5}$$

Therefore, we can define a hypothetical maximum value for x_4, which we will call x_{4max}:

$$x_{4max} = (4\bar{\alpha} - \gamma)/3 \tag{B.6}$$

Because x_4 is constrained to be an integer and x_{4max} is not necessarily an integer, we must also define the actual largest integer that x_4 can be, we will call this value x_{4int}:

$$x_{4int} = \text{floor}[(4\bar{\alpha} - \gamma)/3] = \lfloor (4\bar{\alpha} - \gamma)/3 \rfloor \tag{B.7}$$

Given that the denominator in x_{4max} is equal to three, there are only three possible values of the difference between x_{4max} and x_{4int}: 0, 1/3, or 2/3. In the following we will treat each of these three possibilities individually because they lead to different occupancy distributions, **x**.

Theorem 1.1.1
If $x_{4max} - x_{4int} = 0$ then $\mathbf{x} = [\gamma - x_{4max}, 0, 0, x_{4max}]$

Proof
We will begin by solving for the largest possible size of x_3. Following the same line of reasoning that was used to derive (B.4) we see that:

$$4\bar{\alpha} - 4x_{4max} - 3x_3 \geq \gamma - x_{4max} - x_3 \tag{B.8}$$

Which simplifies to:

$$(4\bar{\alpha} - \gamma - 3x_{4max})/2 \geq x_3 \tag{B.9}$$

And note that $x_{4max} = (4\bar{\alpha} - \gamma)/3$. Therefore, (B.9) simplifies to $0 \geq x_3$, which demonstrates that the largest x_3 can be is zero. Now we will solve for the largest value of x_2:

$$4\bar{\alpha} - 4x_{4max} - 2x_2 \geq \gamma - x_{4max} - x_2 \tag{B.10}$$

Which simplifies to:

$$4\bar{\alpha} - \gamma - 3x_{4max} \geq x_2 \tag{B.11}$$

And again because $x_{4max} = (4\bar{\alpha} - \gamma)/3$, it follows that $0 \geq x_2$. Any remaining species in the assemblage must be singletons – x_1 species. Specifically there will be $\gamma - x_{4max}$ species that occur in only one site given that there are γ species total and x_{4max} species that occur in all four sites.

■

Theorem 1.1.2
If $x_{4max} - x_{4int} = 1/3$ then $\mathbf{x} = [\gamma - x_{4int} - 1, 1, 0, x_{4int}]$.

Proof
We will start by examining how large x_3 can be. Because of the necessary constraint that the unassigned occupancies must be equal to or greater than the remaining number of species to be assigned we arrive at an inequality that is similar to (B.9) only in this case we must exchange x_{4max} with x_{4int}:

$$(4\bar{\alpha} - \gamma - 3x_{4int})/2 \geq x_3 \tag{B.12}$$

Note that $4\bar{\alpha} - \gamma = 3x_{4max}$ therefore (B.12) simplifies to:

$$3(x_{4max} - x_{4int})/2 \geq x_3 \tag{B.13}$$

As stated above $x_{4max} - x_{4int} = 1/3$, after substitution of 1/3 into (B.13) it is clear that $1/2 \geq x_3$.

Therefore because x_3 must be an integer, the largest x_3 can be is zero.

Now we will solve for the largest x_2,

$$4\bar{\alpha} - 4x_{4int} - 3x_{3max} - 2x_2 \geq \gamma - x_{4int} - x_{3max} - x_2 \tag{B.14}$$

Which simplifies to:

$$4\bar{\alpha} - \gamma - 3x_{4int} - 2x_{3max} \geq x_2 \tag{B.15}$$

$$3(x_{4max} - x_{4int}) - 2x_{3max} \geq x_2 \tag{B.16}$$

$$3(1/3) - 2(0) \geq x_2 \tag{B.17}$$

$$1 \geq x_2 \tag{B.18}$$

The remaining unassigned species must be singletons, there will be $\gamma - x_{4int} - 1$ species that occur in only one site given that there are γ species total, x_{4int} species that occur in four sites, and one species that occurs in two sites.

■

Theorem 1.1.3
If $x_{4max} - x_{4int} = 2/3$ then $\mathbf{x} = [\gamma - x_{4int} - 1, 0, 1, x_{4int}]$.

Proof
First note that solving for maximum x_3 leads to (B.12) and (B.13), therefore we will begin by substituting 2/3 for $x_{4max} - x_{4int}$ into (B.13):

$$3(2/3) / 2 \geq x_3 \tag{B.19}$$

$$1 \geq x_3 \tag{B.20}$$

Therefore, at most one species can occur in three of the sites and we can define $x_{3max} = 1$.

Now we will solve for the largest x_2, and we note that this leads to (B.14– 16) with the only exception that $x_{3max} = 1$ and $x_{4max} - x_{4int} = 2/3$ in this case, therefore we will begin by substituting these values into (B.16):

$$3(2/3) - 2(1) \geq x_2 \tag{B.21}$$

$$0 \geq x_2 \tag{B.22}$$

The remaining unassigned species must be singletons, there will be $\gamma - x_{4int} - 1$ species that occur in only one site given that there are γ species total, x_{4int} species that occur in four sites, and one species that occurs in three sites.

■

1.2 - Minimum average turnover and the matching/mismatching components as a function of $\bar{\alpha}$ and γ

Now we will add an additional constraint that richness does not vary between quadrats: $\alpha_i = \bar{\alpha}$ which is necessary to derive expressions for the average turnover ($\overline{T}_J$) as defined by the Jaccard index of dissimilarity for each of the three cases given in the preceding section.

Theorem 1.2.1
If $\mathbf{x} = [\gamma - x_{4max}, 0, 0, x_{4max}]$ then
$\overline{T}_J = 2(\bar{\alpha} - x_{4max}) / (2\bar{\alpha} - x_{4max})$,
a = x_{4max}, and
b = c = $\bar{\alpha} - x_{4max}$.

Proof
There are six possible unique pairwise calculations of turnover in an assemblage of 4 quadrats. We will refer to each of the six comparisons as T_{Jk} for the kth comparison.

T_{Jk} = # of unique species in two quadrats / #of total species between the two quadrats

= $2(\bar{\alpha} - \text{a}) / (2\bar{\alpha} - \text{a})$, where a is the number of species shared between the two quadrats

In the $\mathbf{x}$ under consideration, any pairwise comparisons will result in $x_{4\max}$ species shared. Therefore, each of the six comparisons will result in identical values of T_{Jk}, which indicates that $\bar{T}_J = T_{Jk}$.

The number of species in the first site is $\bar{\alpha}$ and the number of new species gained by also considering the second site is simply the richness of the second site, $\bar{\alpha}$, minus the number of shared species, $x_{4\max}$: $\bar{\alpha} - x_{4\max}$. Therefore:

$$\bar{T}_J = (1/6)\sum_{k=1}^{6} T_{Jk} = T_k = 2(\bar{\alpha} - x_{4\max}) / [\bar{\alpha} + (\bar{\alpha} - x_{4\max})] = 2(\bar{\alpha} - x_{4\max}) / (2\bar{\alpha} - x_{4\max}).$$

With respect to the matching/mismatching components, it should be clear that, a = $x_{4\max}$ and b = c = $\bar{\alpha} - x_{4\max}$.

■

Theorem 1.2.2
If $\mathbf{x} = [\gamma - x_{4\text{int}} - 1, 1, 0, x_{4\text{int}}]$ then
$\bar{T}_J = (1/6)\{2(\bar{\alpha} - x_{4\text{int}} - 1) / (2\bar{\alpha} - x_{4\text{int}} - 1) + 5[2(\bar{\alpha} - x_{4\text{int}}) / (2\bar{\alpha} - x_{4\text{int}})]\}$,
$\mathbf{a} = [x_{4\text{int}} + 1, x_{4\text{int}}, x_{4\text{int}}, x_{4\text{int}}, x_{4\text{int}}, x_{4\text{int}}]$, and
$\mathbf{b} = \mathbf{c} = [\bar{\alpha} - x_{4\text{int}} - 1, \bar{\alpha} - x_{4\text{int}}, \bar{\alpha} - x_{4\text{int}}, \bar{\alpha} - x_{4\text{int}}, \bar{\alpha} - x_{4\text{int}}, \bar{\alpha} - x_{4\text{int}}]$.

Proof
In this case the six pairwise calculations of T_{Jk} will result in one of two values depending on whether or not a given pair of quadrats share more than $x_{4\text{int}}$ species. There will only be a single pair of quadrats that share $x_{4\text{int}} + 1$ species, this pair will have a total of $\bar{\alpha} + \bar{\alpha} - (x_{4\text{int}} + 1)$ species, therefore:

$$T_{Jk} = 2[\bar{\alpha} - (x_{4\text{int}} + 1)] / [2\bar{\alpha} - (x_{4\text{int}} + 1)] \text{ for } k = 1$$

In this comparison, a = $x_{4\text{int}} + 1$ and b = c = $\bar{\alpha} - x_{4\text{int}} - 1$.

The remaining five pairs will only share $x_{4\text{int}}$ species and will have a combined total of $\bar{\alpha} + \bar{\alpha} - x_{4\text{int}}$ species.

$$T_{Jk} = 2(\bar{\alpha} - x_{4\text{int}}) / (2\bar{\alpha} - x_{4\text{int}}) \text{ for } k = 2, 3, 4, 5, 6$$

In these five comparisons, a = $x_{4\text{int}}$ and b = c = $\bar{\alpha} - x_{4\text{int}}$.

$$\bar{T}_J = (1/6)\sum_{k=1}^{6} T_{Jk} = (1/6)\, 2(\bar{\alpha} - x_{4\text{int}} - 1) / (2\bar{\alpha} - x_{4\text{int}} - 1)] + (5/6)\, 2(\bar{\alpha} - x_{4\text{int}}) / (2\bar{\alpha} - x_{4\text{int}})$$

$$\bar{T}_J = (1/6)\{2(\bar{\alpha} - x_{4\text{int}} - 1) / (2\bar{\alpha} - x_{4\text{int}} - 1) + 5[2(\bar{\alpha} - x_{4\text{int}}) / (2\bar{\alpha} - x_{4\text{int}})]\}$$

■

Theorem 1.2.3
If $\mathbf{x} = [\gamma - x_{4\text{int}} - 1, 0, 1, x_{4\text{int}}]$ then
$\overline{T}_J = (1/2)[2(\bar{a} - x_{4\text{int}} - 1) / (2\bar{a} - x_{4\text{int}} - 1) + 2(\bar{a} - x_{4\text{int}}) / (2\bar{a} - x_{4\text{int}})]$,
$\mathbf{a} = [x_{4\text{int}}+1, x_{4\text{int}}+1, x_{4\text{int}}+1, x_{4\text{int}}, x_{4\text{int}}, x_{4\text{int}}]$, and
$\mathbf{b} = \mathbf{c} = [\bar{a} - x_{4\text{int}} - 1, \bar{a} - x_{4\text{int}} - 1, \bar{a} - x_{4\text{int}} - 1, \bar{a} - x_{4\text{int}}, \bar{a} - x_{4\text{int}}, \bar{a} - x_{4\text{int}}]$.

Proof
Again there are only two unique values of T_{Jk} depending on whether the pair of quadrats considered shares $x_{4\text{int}}$ species (three comparisons) or $x_{4\text{int}} + 1$ species (three comparisons). In the latter case there will be a total of $\bar{a} + \bar{a} - (x_{4\text{int}} + 1)$ species:

$T_{Jk} = 2[\bar{a} - (x_{4\text{int}} + 1)] / [2\bar{a} - (x_{4\text{int}} + 1)]$ for $k = 1, 2, 3$

In these three comparisons, a = $x_{4\text{int}} + 1$ and b = c = $\bar{a} - x_{4\text{int}} - 1$.

The other three comparisons will result in only $x_{4\text{int}}$ shared species with a total of $2\bar{a} - x_{4\text{int}}$ species

$T_{Jk} = 2(\bar{a} - x_{4\text{int}}) / (2\bar{a} - x_{4\text{int}})$ for $k = 4, 5, 6$

In these three comparisons, a = $x_{4\text{int}}$ and b = c = $\bar{a} - x_{4\text{int}}$.

From these equations we can formulate the average turnover as:

$$\overline{T}_J = (1/6)\sum_{k=1}^{6} T_{Jk} = (3/6)[2(\bar{a} - x_{4\text{int}} - 1) / (2\bar{a} - x_{4\text{int}} - 1)] + (3/6)\ [2(\bar{a} - x_{4\text{int}} / (2\bar{a} - x_{4\text{int}})]$$

$$\overline{T}_J = (1/2)[2(\bar{a} - x_{4\text{int}} - 1) / (2\bar{a} - x_{4\text{int}} - 1) + 2(\bar{a} - x_{4\text{int}}) / (2\bar{a} - x_{4\text{int}})]$$

■

1.3 - Minimum average turnover as a function of z
In sub-section 1.2, we defined several different formulations of $\overline{T}_J = f(\bar{a}, \gamma)$ which minimized average turnover value. Here we will derive the function $h(z)$ which also minimizes $\overline{T}_J$. This section is necessary because $h(z) \leq f(\bar{a}, \gamma)$ and therefore, a simple reformulation of $f(\bar{a},\gamma)$ in terms of z does not always result in $h(z)$.

Theorem 1.3.1
The minimum value of average turnover is $\overline{T}_J = (2^{2z} - 1) / (2^{2z-1} + 1)$ for $z \in [0,1]$.

Lemma 1.3.2
For a given z-value, the lowest $\overline{T}_J$ will result from an assemblage composed of only x_1 and x_4 species.

Proof
First we must recognize that a given z-value can be achieved by infinitely many different sets of $\bar{\alpha}$ and γ, specifically: $z = \log_2(\gamma/\bar{\alpha})/2 = \log_2(\gamma^*/\bar{\alpha}^*)/2$ where $\gamma^* = m\gamma$, $\bar{\alpha}^* = m\bar{\alpha}$, and m is any positive number. Although $\bar{\alpha}^*$ and γ^* have the same z as $\bar{\alpha}$ and γ, it should be clear that the difference equations $(4\bar{\alpha}-\gamma)/3-\lfloor(4\bar{\alpha}-\gamma)/3\rfloor$ and $m(4\bar{\alpha}-\gamma)/3-\lfloor m(4\bar{\alpha}-\gamma)/3\rfloor$ may or may not be equal. These particular difference equations are of interest because their value determines which formulation of $f(\bar{\alpha}, \gamma)$ will be used to minimize $\overline{T}_J$ (see sub-sections 1.1 and 1.2). In sub-section 1.1, it was noted that the difference equations will be equal to 0, 1/3, or 2/3 depending on how constrained $x_{4\max}$ was by the requirement to be an integer. A difference of zero implies that $x_{4\max}$ is as large as possible which results in the lowest possible value of average turnover given z. Furthermore, if m is a multiple of three (i.e., $m = 3n$ where n is a positive integer) then $m(4\bar{\alpha}-\gamma)/3-\lfloor m(4\bar{\alpha}-\gamma)/3\rfloor = n(4\bar{\alpha}-\gamma)-\lfloor n(4\bar{\alpha}-\gamma)\rfloor = 0$ this follows because $n(4\bar{\alpha} - \gamma)$ must be an integer given that we defined n, $\bar{\alpha}$, and γ as positive integers. This demonstrates that for any values of α and γ there are corresponding values of $\bar{\alpha}^* = 3n\bar{\alpha}$ and $\gamma^* = 3n\gamma$ that have the same z and result in an occupancy distribution composed of only x_1 and x_4 species (i.e., $\mathbf{x} = [\gamma^* - 3nx_{4\max}, 0, 0, 3nx_{4\max}]$). Given that we are attempting to minimize turnover we want to have as many x_4 species as possible, and therefore we should derive $\overline{T}_J = h(z)$ under the assumption that the occupancy distribution is composed of only x_1 and x_4 species.

■

Proof of Theorem 1.3.1
In 1.2.1 we demonstrated that if $\mathbf{x} = [\gamma - x_{4\max}, 0, 0, x_{4\max}]$ then $\overline{T}_J = 2(\bar{\alpha} - x_{4\max}) / (2\bar{\alpha} - x_{4\max})$. Therefore we can reformulate $\overline{T}_J = 2(\bar{\alpha} - x_{4\max}) / (2\bar{\alpha} - x_{4\max})$ in terms of z, as follows:

$$\overline{T}_J = 2(\bar{\alpha} - x_{4\max}) / (2\bar{\alpha} - x_{4\max})$$

$$\overline{T}_J = 2[\bar{\alpha} - (4\bar{\alpha} - \gamma)/3] / [2\bar{\alpha} - (4\bar{\alpha} - \gamma)/3]$$

Because $z = \log_2(\gamma/\bar{\alpha})/2$ we can solve for γ as, $\gamma = \bar{\alpha}2^{2z}$, and after substituting this into the equation for $\overline{T}_J$ we see that:

$$\overline{T}_J = 2[\bar{\alpha} - (4\bar{\alpha} - \bar{\alpha}2^{2z})/3] / [2\bar{\alpha} - (4\bar{\alpha} - \bar{\alpha}2^{2z})/3]$$

$$\overline{T}_J = \left(\frac{6\bar{\alpha}}{3} - \frac{8\bar{\alpha}}{3} + \frac{\bar{\alpha}2^{2z+1}}{3}\right) \Big/ \left(\frac{6\bar{\alpha}}{3} - \frac{4\bar{\alpha}}{3} + \frac{\bar{\alpha}2^{2z}}{3}\right)$$

$\overline{T}_J = (\bar{\alpha}2^{2z+1} - 2\bar{\alpha}) / (\bar{\alpha}2^{2z} + 2\bar{\alpha})$

$\overline{T}_J = (2^{2z} - 1) / (2^{2z-1} + 1)$

■

2 - Maximizing Pairwise Turnover

Average turnover will be maximal when as many species as possible are at the lowest occupancy levels. For example, the maximum average turnover of 1 is only possible when the entire community is composed of singletons – x_1 species. Therefore, the first question to address, is if the entire community is composed of x_1 species how many x_1 species are there? Equations B.1 and B.2 indicate that, $x_1 = \gamma$ and $x_1 = 4\bar{\alpha}$ if the community is composed of only singletons. These two statements imply that this can only be possible if $\gamma = 4\bar{\alpha}$. Below we derive the occupancy distributions, **x**, that maximize average turnover when γ is any value ranging from $4\bar{\alpha}$ to $\bar{\alpha}$. We also provide the conversion of each range of γ values into a range of z-values.

2.1 - Occupancy distributions that maximize turnover for a given $\bar{\alpha}$ and γ

Theorem 2.1.1
If $4\bar{\alpha}/2 \leq \gamma \leq 4\bar{\alpha}$ (i.e., $0.5 \leq z \leq 1$) then average turnover is maximal when $\mathbf{x} = [2\gamma - 4\bar{\alpha}, 4\bar{\alpha} - \gamma, 0, 0]$.

Proof
As noted, the maximum value of 1 for average turnover only occurs when $\gamma = 4\bar{\alpha}$ and therefore all species in the community are x_1 species. Now consider the situation in which γ is slightly less than $4\bar{\alpha}$ (we will define how much less shortly), then there must be species at occupancy levels other than x_1. We wish again to maximize turnover, therefore we will place as many species as possible into the x_1 occupancy level and the remaining species will be placed in the x_2 occupancy level. If there are only x_1 and x_2 species, (1) and (2) simplify to: $x_1 + x_2 = \gamma$ and $x_1 + 2x_2 = 4\bar{\alpha}$. After substitution of terms and rearrangement:

$x_1 = 2\gamma - 4\bar{\alpha}$
$x_2 = 4\bar{\alpha} - \gamma$

These equations were derived by considering a γ value less than $4\bar{\alpha}$, now we will define what value of γ these equations will hold over. If we consider the equation for x_1, we can see that x_1 will only be a non–negative integer (i.e., a reasonable value) when $\gamma \geq 4\bar{\alpha}/2$. Note that when $\gamma = 4\bar{\alpha}/2$, $x_1 = 0$ and $x_2 = \gamma$, we will refer to this situation as the 'doubleton community' because all of the species are of the x_2 occupancy level. Also note, if $\gamma = 4\bar{\alpha}$ (as in the singleton community) then our equations for x_1 and x_2 produce satisfactory results, namely, $x_1 = \gamma$ and $x_2 = 0$. Therefore, if $4\bar{\alpha}/2 \leq \gamma \leq 4\bar{\alpha}$ then average turnover is maximal when $\mathbf{x} = [2\gamma - 4\bar{\alpha}, 4\bar{\alpha} - \gamma, 0, 0]$.

■

Theorem 2.1.2
If $4\bar{\alpha}/3 \leq \gamma < 4\bar{\alpha}/2$ (i.e., $\log_2(4/3)/2 \leq z < 0.5$) then average turnover is maximal when $\mathbf{x} = [0, 3\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 2\gamma, 0]$.

Proof
Consider again the doubleton community (see above), in which $\gamma = 4\bar{\alpha}/2$. If γ was slightly less than $4\bar{\alpha}/2$ (we will define how much less shortly), species at occupancy levels other than x_2 must exist in the community. Because we are attempting to maximize turnover, the other occupancy level/s could be x_1 and/or x_3. It should be clear that adding an x_4 species would contribute too many shared species to maximize turnover. Also if the assemblage is composed of only x_1 and x_2 species then $\gamma \in [4\bar{\alpha}/2, 4\bar{\alpha}]$ and the results from *Theorem 2.1.1* hold. Therefore, the question arises of whether or not the assemblage should be composed of x_1, x_2 and x_3 species or only x_2 and x_3 species.

Here we will quickly prove that turnover will be maximized by considering a community composed of only x_2 and x_3 species. Consider two x_2 species arranged such that each quadrat has a richness of one. There are a total of two shared species in this case. If we exchanged these two x_2 species for one x_1 and one x_3 species and arranged them such that quadrat richness is still one, then the total number of shared species will be three. To maximize turnover, we must minimize the number of shared species all else being equal. Therefore, whenever $4\bar{\alpha}$ and γ are such that an x_1 and x_3 could be placed in the community, average turnover will be larger if two x_2 species are considered in the community instead. This suggests that if we wish to maximize turnover we should not consider assemblages in which x_1 and x_3 species co-occur. Therefore, we will assume that the community only contains x_2 or x_3 species, in which case equations (B.1) and (B.2) simplify to: $x_2 + x_3 = \gamma$ and $2x_2 + 3x_3 = 4\bar{\alpha}$. After substitution of terms and rearrangement:

$x_2 = 3\gamma - 4\bar{\alpha}$
$x_3 = 4\bar{\alpha} - 2\gamma$

We can define the minimum value of γ that these equations will apply to by examining the equation for x_2. This equation will only produce non–negative integer values when $\gamma \geq 4\bar{\alpha}/3$. At the boundary when $\gamma = 4\bar{\alpha}/3$, $x_2 = 0$ and $x_3 = \gamma$, we will refer to this situation as the ‘tripleton community’. Therefore, if $4\bar{\alpha}/3 \leq \gamma < 4\bar{\alpha}/2$ then average turnover is maximal when $\mathbf{x} = [0, 3\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 2\gamma, 0]$.

■

Theorem 2.1.3
If $\bar{\alpha} \leq \gamma < 4\bar{\alpha}/3$ (i.e., $0 \leq z < \log_2(4/3)/2$) then average turnover is maximal when $\mathbf{x} = [0, 0, 4\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 3\gamma]$.

Proof
Consider again the tripleton community, in which $\gamma = 4\bar{\alpha}/3$. If gamma was slightly less than $4\bar{\alpha}/3$, then x_4 species would have to be present in the community. Therefore, consider the community which is composed only of x_3 and x_4 species, equations (B.1) and (B.2) simply to $x_3 + x_4 = \gamma$ and $3x_3 + 4x_4 = 4\bar{\alpha}$. After substitution of terms and rearrangement:

$x_3 = 4\gamma - 4\bar{\alpha}$
$x_4 = 4\bar{\alpha} - 3\gamma$

We can define the minimum value of γ that these equations will apply to by examining the equation for x_3. This equation will only produce non–negative integer values when $\gamma \geq \bar{\alpha}$. At the boundary when $\gamma = \bar{\alpha}$, $x_3 = 0$ and $x_4 = \gamma$. Therefore, if $\bar{\alpha} \leq \gamma < 4\bar{\alpha}/3$ then average turnover is maximal when $\mathbf{x} = [0, 0, 4\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 3\gamma]$.

■

2.2 - Maximum average turnover and matching/mismatching components as a function of $\bar{\alpha}$, γ, and z

Before we derive expressions that maximize $\overline{T}_J$, we must prove two lemmas that guide how x_2 species should be arranged in the presence-absence matrix to maximize $\overline{T}_J$. In general, it is important to consider that two communities may have identical occupancy distributions but different values of $\overline{T}_J$. In the preceding sections this fact was not a concern because there was only a single possible presence-absence matrix which could be composed of only x_1, x_4, and possibly one x_2 or x_3 species given that each site had to contain exactly $\bar{\alpha}$ species. Fixed quadrat richness does not place as strong of a constraint on the arrangement of species in an assemblage composed of primarily x_2 or x_3 species which may be arranged in different ways and still result in the same column sums. A simple example demonstrating this is provided in Table B3. In the table there are two hypothetical communities both with the occupancy distribution, $\mathbf{x} = [2, 3, 0, 0]$, but the communities differ in terms of their $\overline{T}_J$ value.

Table B3. Two example species presence-absence matrices that demonstrate that $\overline{T}_J$ may differ for two assemblages with the same $\mathbf{x}$. A grey shaded cell represents a species presence and a white cell represents a species absence.

Community	A					B			
Quadrat	1	2	3	4		1	2	3	4
species 1									
species 2									
species 3									
species 4									
species 5									
Richness	2	2	2	2		2	2	2	2
$\overline{T}_J$	7/9 = 0.778					5/6 = 0.833			

There are many different possible arrangements of x_2 or x_3 species, and therefore it is necessary that we identify what arrangements of species maximize $\overline{T}_J$ for a given $\mathbf{x}$. Our simple example in Table B3 suggests one possible way to begin addressing this problem. If we consider the set of the six pairwise comparisons for each assemblage, we can see that community B, which has the larger value of $\overline{T}_J$, has a lower amount of variance in its shared species distribution than community A. Specifically the vector of shared species for each pairwise comparison in community A is $\mathbf{a}_A$ = [1,0,0,0,0,2] and for community B is $\mathbf{a}_B$ = [1,0,0,1,0,1]. This demonstrates that both assemblages possess a total of 3 pairwise shared species occurrences, but that these occurrences are more evenly distributed in community B than in A.

Lemma 2.2.1
If two communities have the same occupancy distribution the one with lower variance in the distribution of shared species will have a larger value of $\overline{T}_J$.

Proof
Consider two assemblages, A and B, with identical values of γ and $\bar{\alpha}$. The assemblages also have identical shared species distributions with the exception of two of the six pairwise comparisons. In community A, the number of shared species in the two comparisons of interest is equal to a, in community B the shared number of species in the two comparisons is a – 1 and a + 1 respectively where a is a positive integer greater than 1. Both communities have the same total number of shared species occurrences, but the community A has a slightly lower variance in its distribution of shared species when compared with community B. To prove that this lower variance will result in a larger value of $\overline{T}_J$ we only need to consider the sum of the two T_{Jk} terms resulting from the comparisons in which the two communities differ in their distribution of shared species. The sum of the other four T_{Jk} terms must be equal between the two communities given that they have the same shared species distribution for these comparisons. Therefore, we must prove that the following is true:

$$T_{JA1} + T_{JA2} > T_{JB1} + T_{JB2}$$
$$2\left(\frac{2\overline{\alpha} - 2\mathrm{a}}{2\overline{\alpha} - \mathrm{a}}\right) > \left(\frac{2\overline{\alpha} - 2(\mathrm{a}+1)}{2\overline{\alpha} - (\mathrm{a}+1)} + \frac{2\overline{\alpha} - 2(\mathrm{a}-1)}{2\overline{\alpha} - (\mathrm{a}-1)}\right)$$

The above inequality asserts that the sum of the two T_{Jk} terms in the community without variance in its shared species (community A) is greater than the sum of the two T_{Jk} terms in the community with variance in its shared species (community B).

To simplify the equation we will perform a change of variables, $y = 2\bar{\alpha}$ and we will expand out the factions by multiplying both sides by $(y - \mathrm{a})(y - \mathrm{a} - 1)(y - \mathrm{a} + 1)$. When this is done the LHS expands to:

$$2(y^3 - 2\mathrm{a}^3 - 4y^2\mathrm{a} + 5y\mathrm{a}^2 - y + 2\mathrm{a})$$

The first fraction in the RHS expands to

$$y^3 - 2\mathrm{a}^3 - 4y^2\mathrm{a} + 5y\mathrm{a}^2 - y^2 + y\mathrm{a} - 2y + 2\mathrm{a}$$

and the second fraction in the RHS expands to

$y^3 - 2a^3 - 4y^2a + 5ya^2 + y^2 - ya - 2y + 2a$

Therefore, when we combine both parts of the RHS we see that it is equal to

$2(y^3 - 2a^3 - 4y^2a + 5ya^2 - 2y + 2a)$

Now bringing the LHS and RHS back together we see that the original formula implied that

$2(y^3 - 2a^3 - 4y^2a + 5ya^2 - y + 2a) > 2(y^3 - 2a^3 - 4y^2a + 5ya^2 - 2y + 2a)$

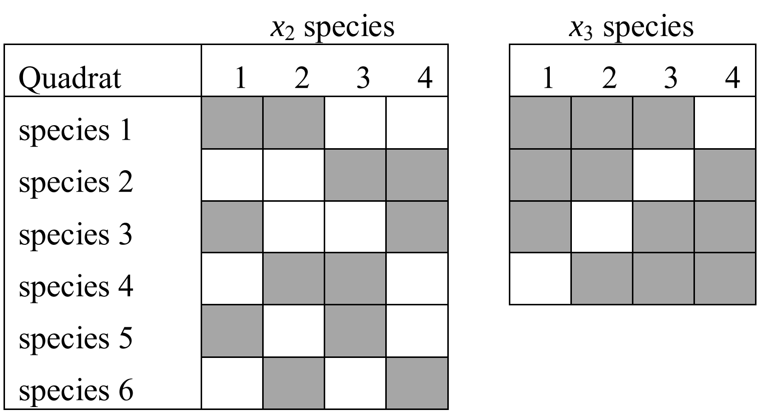
And after crossing off like terms, the inequality reduces to 1 < 2 which is obviously true.

■

Lemma 2.2.2
If x_2 or x_3 species are in an assemblage, the function $h(z)$ which maximizes $\overline{T}_J$ must be based upon the assumption that the x_2 species contribute $x_2/6$ and the x_3 species contribute $x_3/2$ shared species to each pairwise comparison.

Proof
From *Lemma 2.2.1* we know that to maximize $\overline{T}_J$ the x_2 and x_3 species must be arranged to minimize variance in the distribution of shared species. The minimum amount of variance in a distribution of shared species is zero, in which case $\overline{T}_J = T_{Jk}$. The presence-absence matrices in Table B4 display the arrangement of a set of x_2 and a set x_3 species that result in zero variance in the shared species distribution and quadrat richness is constant. These arrangements provide a basis for calculating how many shared species will be contributed in the pairwise comparisons.

Table B4. A presence-absence matrix of a set of six x_2 species and a set of four x_3 species in which there is zero variance in the distribution of shared species occurrences. In the set of x_2 species, each quadrat contributes 1 shared species in every pairwise comparison (i.e., a = 1), and in the set of x_3 species, each quadrat contributes 2 shared species in every pairwise comparison (i.e., a = 2). A grey shaded cell represents a species presence and a white cell represents a species absence.



The sets of species in Table B4 represent the simplest arrangement of x_2 and x_3 species with zero variance in the distribution of shared species and constant quadrat richness. The fact that each quadrat has equal richness is critical because it allows us to individually consider the contribution of each level of occupancy to the total number of shared species.

Now we will prove why h(z) should be based upon the assumption that if x_2 species are present the number of shared species contributed to each pairwise comparison by these species is $x_2/6$. The arrangement of x_2 species given in Table B4 demonstrates that for every six x_2 species a = 1. This suggests that when x_2 is a multiple of six that the number of shared species in a single pairwise comparison is equal to:

a = $g(\bar{\alpha}, \gamma)/6$ where $x_2 = g(\bar{\alpha}, \gamma)$.

Although this definition of a is only applicable to a limited set of $\bar{\alpha}$ and γ values, specifically those in which $g(\bar{\alpha}, \gamma)/6$ is an integer, it holds for any value of z. This is because for any z-value calculated from $\bar{\alpha}$ and γ, there also exists $\bar{\alpha}^* = m\bar{\alpha}$ and $\gamma^* = m\gamma$ that result in the same z but for which $g(\bar{\alpha}^*, \gamma^*) = x_2^*$ is a multiple of six.

Therefore for a given z-value,

$$\overline{T}_J = \frac{2\overline{\alpha}^* - 2\mathrm{a}}{2\overline{\alpha}^* - \mathrm{a}} = \frac{2\overline{\alpha}^* - 2g(\overline{\alpha}^*, \gamma^*)/6}{2\overline{\alpha}^* - g(\overline{\alpha}^*, \gamma^*)/6} = \frac{2m\overline{\alpha} - 2g(m\overline{\alpha}, m\gamma)/6}{2m\overline{\alpha} - g(m\overline{\alpha}, m\gamma)/6}$$

If we consider that both expressions of $x_2 = g(\bar{\alpha}, \gamma)$ described in *Theorems 2.1.1* and *2.1.2* are linear equations then it should be clear that we can factor m out of $g(m\bar{\alpha}, m\gamma)$. Therefore,

$$\overline{T}_J = \frac{2\overline{\alpha} - 2g(\overline{\alpha}, \gamma)/6}{2\overline{\alpha} - g(\overline{\alpha}, \gamma)/6}$$

This demonstrates that for a given z-value the function $\overline{T}_J = h(z)$ should be based upon the assumption that a = $g(\bar{\alpha}, \gamma)/6 = x_2/6$ even if this is a non-integer value. An identical line of reasoning can be used to show that $h(z)$ must be based upon the assumption that the x_3 species contribute $x_3/2$ shared species to every pairwise comparison.

■

Theorem 2.2.3

If $4\bar{\alpha}/2 \leq \gamma \leq 4\bar{\alpha}$ (i.e., $0.5 \leq z \leq 1$) then $\overline{T}_J = (2^{2z-1} + 1)/(2^{2z-2} + 2)$, and when $x_2/6$ is an integer, $\overline{T}_J = (2\bar{\alpha} + \gamma) / (4\bar{\alpha} + \gamma/2)$, a = $2\bar{\alpha}/3 - \gamma/6$, and b = c = $\bar{\alpha}/3 + \gamma/6$.

Proof

We saw that in *Theorem 2.1.1* that when $4\bar{\alpha}/2 \leq \gamma \leq 4\bar{\alpha}$ that $\mathbf{x} = [2\gamma - 4\bar{\alpha}, 4\bar{\alpha} - \gamma, 0, 0]$ and because the x_1 species will not contribute any shared species in the pairwise comparisons we only need to calculate how many shared species the $4\bar{\alpha} - \gamma$, x_2 species will contribute in the pairwise comparisons. In *Lemma 2.2.2* we demonstrated that the derivation of $h(z) = \overline{T}_J$ should be based upon the assumption that a = $x_2/6$. If $x_2/6$ is an integer then we can formulate $\overline{T}_J = f(\bar{\alpha}, \gamma)$ as follows:

$$\overline{T}_J = f(\bar{\alpha},\gamma) = \frac{2\bar{\alpha} - 2x_2/6}{2\bar{\alpha} - x_2/6} = \frac{2\bar{\alpha} - 2(4\bar{\alpha} - \gamma)/6}{2\bar{\alpha} - (4\bar{\alpha} - \gamma)/6} = \frac{\frac{1}{3}(2\bar{\alpha} + \gamma)}{\frac{1}{3}(4\bar{\alpha} + \gamma/2)} = \frac{2\bar{\alpha} + \gamma}{4\bar{\alpha} + \gamma/2}$$

Obviously in this case, a = $(4\bar{\alpha} - \gamma)/6 = 2\bar{\alpha}/3 - \gamma/6$ and b = c = $(2\bar{\alpha} + \gamma)/6 = \bar{\alpha}/3 + \gamma/6$.

We currently lack a derivation of $f(\bar{\alpha}, \gamma)$, a, b, and c when $x_2/6$ is a non-integer due to the complexity of specifying what arrangement the x_2 species must take in the presence-absence matrix.
To derive $\overline{T}_J = h(z)$ we can substitute $\gamma = 2^{2z}\bar{\alpha}$ into $f(\bar{\alpha}, \gamma)$,

$$\overline{T}_J = \frac{2\bar{\alpha} + 2^{2z}\bar{\alpha}}{4\bar{\alpha} + 2^{2z}\bar{\alpha}/2} = \frac{2 + 2^{2z}}{4 + 2^{2z-1}} = (2^{2z-1} + 1)/(2^{2z-2} + 2)$$

As noted in *Lemma 2.2.2* this last expression will hold whether $x_2/6$ is an integer or not.

■

Theorem 2.2.4
If $4\bar{\alpha}/3 \le \gamma < 4\bar{\alpha}/2$ (i.e., $\log_2(4/3)/2 \le z < 0.5$) then $\overline{T}_J = (2^{2z} - \frac{2}{3})/(2^{2z-1} + \frac{2}{3})$, and when $x_2/6 + x_3/2$ is an integer, $\overline{T}_J = (\gamma - 2\bar{\alpha}/3) / (\gamma/2 + 2\bar{\alpha}/3)$, a = $4\bar{\alpha}/3 - \gamma/2$, and b = c = $\gamma/2 - \bar{\alpha}/3$.

Proof
We saw that in *Theorem 2.1.2* that when $4\bar{\alpha}/3 \le \gamma < 4\bar{\alpha}/2$ that $\mathbf{x} = [0, 3\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 2\gamma, 0]$ and in *Lemma 2.2.2* we proved that the derivation of $h(z) = \overline{T}_J$ should be based upon the assumption that a = $x_2/6 + x_3/2 = (3\gamma - 4\bar{\alpha})/6 + (2\bar{\alpha} - \gamma) = 4\bar{\alpha}/3 - \gamma/2$. If $x_2/6 + x_3/2$ is an integer then we can formulate $\overline{T}_J = f(\bar{\alpha}, \gamma)$ as follows:

$$\overline{T}_J = f(\bar{\alpha},\gamma) = \frac{2\bar{\alpha} - 2(x_2/6 + x_3/2)}{2\bar{\alpha} - (x_2/6 + x_3/2)} = \frac{2\bar{\alpha} - 2(4\bar{\alpha}/3 - \gamma/2)}{2\bar{\alpha} - (4\bar{\alpha}/3 - \gamma/2)} = \frac{\gamma - 2\bar{\alpha}/3}{\gamma/2 + 2\bar{\alpha}/3}$$

Obviously in this case, a = $4\bar{\alpha}/3 - \gamma/2$ and b = c = $(\gamma - 2\bar{\alpha}/3)/2 = \gamma/2 - \bar{\alpha}/3$.

We currently lack a derivation of $f(\bar{\alpha}, \gamma)$, a, b, and c when $x_2/6 + x_3/2$ is a non-integer due to the complexity of specifying what arrangement the x_2 and x_3 species must take in the presence-absence matrix.

To derive $\overline{T}_J = h(z)$ we can substitute $\gamma = 2^{2z}\bar{\alpha}$ into $f(\bar{\alpha}, \gamma)$,

$$\overline{T}_J = \frac{2^{2z}\bar{\alpha} - 2\bar{\alpha}/3}{2^{2z}\bar{\alpha}/2 + 2\bar{\alpha}/3} = \frac{2^{2z} - \frac{2}{3}}{2^{2z-1} + \frac{2}{3}}$$

As noted in *Lemma 2.2.2* this last expression will hold whether $x_2/6 + x_3/2$ is an integer or not.

■

Theorem 2.2.5

If $\bar{\alpha} \le \gamma < 4\bar{\alpha}/3$ (i.e., $0 \le z < \log_2(4/3)/2$) then $\overline{T}_J = 2 - 2^{1-2z} = 2(\gamma - \overline{\alpha})/\gamma$, a = $2\bar{\alpha} - \gamma$, and b = c = $\gamma - \bar{\alpha}$.

Proof

We saw that in *Theorem 2.1.3* that when $\bar{\alpha} \le \gamma < 4\bar{\alpha}/3$ that $\mathbf{x} = [0, 0, 4\gamma - 4\bar{\alpha}, 4\bar{\alpha} - 3\gamma]$ and in *Lemma 2.2.2* we proved that the derivation of $h(z) = \overline{T}_J$ should be based upon the assumption that a = $x_3/2 + x_4 = (4\gamma - 4\bar{\alpha})/2 + (4\bar{\alpha} - 3\gamma) = 2\bar{\alpha} - \gamma$. Because $\bar{\alpha}$ and γ are integers, $2\bar{\alpha} - \gamma$ will be an integer and we can formulate $\overline{T}_J = f(\bar{\alpha}, \gamma)$ as follows:

$$\overline{T}_J = f(\overline{\alpha}, \gamma) = \frac{2\overline{\alpha} - 2(x_3/2 + x_4)}{2\overline{\alpha} - (x_3/2 + x_4)} = \frac{2\overline{\alpha} - 2(2\overline{\alpha} - \gamma)}{2\overline{\alpha} - (2\overline{\alpha} - \gamma)} = \frac{2(\gamma - \overline{\alpha})}{\gamma}$$

Obviously in this case, a = $2\bar{\alpha} - \gamma$ and b = c = $2(\gamma - \bar{\alpha})/2 = \gamma - \bar{\alpha}$. To derive $\overline{T}_J = h(z)$ we can substitute $\gamma = 2^{2z}\bar{\alpha}$ into $f(\bar{\alpha}, \gamma)$,

$$\overline{T}_J = \frac{2(2^{2z}\overline{\alpha} - \overline{\alpha})}{2^{2z}\overline{\alpha}} = \frac{2^{2z} - 2}{2^{2z}} = 2 - 2^{1-2z}$$

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Literature Cited

Legendre, P. and L. Legendre. 1998. Numerical ecology. Elsevier, Boston, Mass., USA.