Ecological Archives **M081-019-A1**

Nathan L. Stephenson, Phillip J. van Mantgem, Andrew G. Bunn, Howard Bruner, Mark E. Harmon, Kari B. O'Connell, Dean L. Urban, and Jerry F. Franklin. 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. *Ecological Monographs* 81:527–555.

APPENDIX A

Determining relative contributions of proximate causes to differences in mortality rates.

Let "group *ij*" represent LH group *ij* (shade-tolerance class *i*, adult stature class *j*). "Group *ij* proportion" (p_{ij}) is the fraction of a forest's trees found in group *ij*; by definition, $\sum_{i,j} p_{ij} = 1$.

"Group *ij* mortality rate" (m_{ij}) is the group-specific mortality rate of trees in group *ij*. Below, variables indicated by upper case letters apply to the entire forest community (summed across all LH groups); variables indicated by lower case letters apply to trees within the individual LH groups.

$M = \frac{1}{N}\sum_{i,j} d_{ij}$, where *M* is community-wide mortality rate, d_{ij} is the total number of trees that die per unit time in group *ij*, and *N* is the total number of living trees in the forest at the start of the mortality measurement interval. But $d_{ij} = n_{ij} m_{ij}$, where n_{ij} is the number of living trees in group *ij* at the start of the interval. Thus,

$$
\begin{aligned}
M &= \frac{1}{N}\sum_{i,j} n_{ij} m_{ij} \\
&= \sum_{i,j} p_{ij} m_{ij}
\end{aligned}
\qquad \text{(A.1)}
$$

Let $\Delta M = M^{high} - M^{low}$, the difference in mortality rates between the high- and low-mortality forests. From Eq. A.1 it is quickly evident that $\Delta M = \sum_{i,j} (p_{ij}^{high} m_{ij}^{high} - p_{ij}^{low} m_{ij}^{low}) = \sum_{i,j} \Delta c_{ij}$, where Δc_{ij} is the difference between $p_{ij}^{high} m_{ij}^{high}$ (the absolute contribution of *high* group *ij* to M^{high}) and $p_{ij}^{low} m_{ij}^{low}$ (the absolute contribution of corresponding *low* group *ij* to M^{low}). We now calculate what amount of Δc_{ij} can be attributed to differences between the *high* and *low* forests in group *ij* proportions (differences in p_{ij}). If the only difference between *high* and *low* forests were in group *ij* proportions (that is, if group *ij* mortality rates were a constant m_{ij}^{low} for both the *high* and *low* forests), only differences in group *ij* proportions would contribute to Δc_{ij}, in the amount of $m_{ij}^{low}(p_{ij}^{high} - p_{ij}^{low})$. However, if group *ij* mortality rates and group *ij* proportions both differ between *high* and *low* forests, some of Δc_{ij} will be equally attributable to both: $(p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} - m_{ij}^{low})$. This term represents contributions to Δc_{ij} that could not have been produced by difference in group *ij* proportions alone, or by differences in group *ij* mortality rates alone. Thus, $\Delta^p c_{ij}$, the absolute amount of Δc_{ij} that is attributable to differences in *high* and *low* group *ij* proportions, is the amount that can be attributed to differences in p_{ij} alone plus half the amount that is equally attributable to differences in both p_{ij} and m_{ij}:

$$\begin{aligned} \Delta^p c_{ij} &= m_{ij}^{low}(p_{ij}^{high} - p_{ij}^{low}) + (p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} - m_{ij}^{low})/2 \\ &= (p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} + m_{ij}^{low})/2 \end{aligned} \tag{A.2}$$

Note that $\Delta^p c_{ij}$ reduces to the difference between the proportions, $p_{ij}^{high} - p_{ij}^{low}$, multiplied by the average of *high* and *low* group *ij* mortality rates, $(m_{ij}^{high} + m_{ij}^{low})/2$.

Summing Eq. A.2 across all groups yields $\Delta^p M$, the absolute difference in community-wide mortality rates between the *high* and *low* forests that is directly attributable to differences in group *ij* proportions:

$$\Delta^p M = \sum_{i,j}(p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} + m_{ij}^{low})/2. \tag{A.3}$$

Finally, the relative amount of the difference in community-wide mortality rates between the two forests that is directly attributable to differences in group *ij* proportions is $\lambda = \Delta^p M / \Delta M$, or

$$\lambda = \frac{\sum_{i,j}(p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} + m_{ij}^{low})}{2(M^{high} - M^{low})}. \tag{A.4}$$

Similar derivation shows that the relative amount that is directly attributable to differences in group *ij* mortality rates is

$$\mu = \frac{\sum_{i,j}(m_{ij}^{high} - m_{ij}^{low})(p_{ij}^{high} + p_{ij}^{low})}{2(M^{high} - M^{low})}. \tag{A.5}$$

When LH-group-specific mortality rates are compared between forests (see that main text), Eqs. A.4 and A.5 are used to calculate the relative contributions of GS-group proportions and GS-group-specific mortality rates to the difference in LH-group-specific mortality rates. In this case, p_{ij} is the proportion of trees, and m_{ij} is the annual mortality rate, in GS group *ij* (growth-rate class *i*, diameter class *j*), and *M* is LH-group-specific mortality rate.

To demonstrate their use and interpretation, we apply Eqs. A.4 and A.5 to two hypothetical forests (Table A1). At the first census (t = 0), each forest contained 1000 living trees, which can be segregated into four different combinations of life-history groups *i* and *j* (e.g., *i* represents shade tolerance class [1 = tolerant species, 2 = intolerant species] and *j* represents adult stature class [1 = canopy species, 2 = subcanopy species]). For each forest, proportions of trees belonging to each combination of life-history groups (p_{ij}) are easily calculated; for example, at t = 0 in the high-mortality forest 300 trees out of the 1000 belong to group 1,1, yielding a fractional proportion of p_{11} = 0.300. As they must, group proportions sum to 1 for each forest. Assuming, for simplicity, that the second census (t = 1) occurred one year after the first, group-specific mortality rates (m_{ij}) are also easily calculated; for example, in the high-mortality forest three of the 300 trees belonging to group 1,1 died, yielding a group-specific mortality rate of m_{11} = 1.000% yr^{-1}. Group proportions and group-specific mortality rates are used to calculate the contributions of each group *i,j* to the numerators of Eqs. A.4 and A.5; these contributions are then summed to calculate the numerators of the equations (Table A1). The community-wide mortality rates (required for calculating the denominators) are 2% yr^{-1} and 1% yr^{-1}, respectively, for the high- and low-mortality forests (20 and 10 tree deaths, respectively, each out of 1000 trees). The denominators of Eqs. A.4 and A.5 are therefore 2(2 - 1) = 2, and thus $\lambda = -0.4166/2 = -0.2083$ and $\mu = 2.4166/2 = 1.2083$ (or, expressed as in Table 2 of the main text, $\lambda \approx -21\%$ and $\mu \approx 121\%$). As they must, $\lambda + \mu = 1$ (or 100%).

In this example, the negative value of λ (the relative contribution of differences in group proportions to the difference in community-wide mortality rates between the two forests) reflects the fact that, relative to the low-mortality forest, the high-mortality forest has a smaller proportion of trees in groups with high group-specific mortality rates (Table A1). Thus, differences in group proportions between the two forests act to reduce the mortality rate of the high-mortality forest relative to the low-mortality forest. However, as indicated by the large positive μ, this reduction is overwhelmed by the consistently higher group-specific mortality rates in the high-mortality forest (Table A1). The difference in community-wide mortality rates between the two forests therefore is entirely a consequence of higher group-specific mortality rates in the high-mortality forest.

TABLE A1: Data for two hypothetical forests, illustrating the use of Eqs. A.4 and A.5.

Group		# of living trees at t=0		# of dead trees at t=1		p_{ij}		m_{ij} (% yr^{-1})		Contribution of group *i,j* to the numerator of eq. A.4 $(p_{ij}^{high} - p_{ij}^{low})(m_{ij}^{high} + m_{ij}^{low})$	Contribution of group *i,j* to the numerator of eq. A.5 $(m_{ij}^{high} - m_{ij}^{low})(p_{ij}^{high} + p_{ij}^{low})$
i	*j*	High*	Low*	High	Low	High	Low	High	Low		
1	1	300	200	3	1	0.300	0.200	1.000	0.500	0.1500	0.2500
1	2	300	200	5	2	0.300	0.200	1.666···	1.000	0.2666···	0.3333···
2	1	200	300	5	3	0.200	0.300	2.500	1.000	-0.3500	0.7500
2	2	200	300	7	4	0.200	0.300	3.500	1.333···	-0.4833···	1.0833···
Sums		1000	1000	20	10	1.000	1.000	--	--	-0.4166···	2.4166···

* "High" and "Low" indicate, respectively, the forests with high and low community-wide mortality rates.

Note: See the text for further explanation.