Fig. S1. Relative uncertainty $\Sigma(x)$ of the steady state concentration $c(x)$ for the diffusion-degradation model with disorder in one dimension (1). (A,B) The symbols indicate results from numerical calculations in which steady-state gradients were calculated for many (typically 100,000) realizations of the disorder. The lines show the corresponding analytical results (8) for $\Sigma(x)$. The red lines show $\Sigma(x)$ if only $D$ is fluctuating, the blue lines if only $k$ is fluctuating, the green lines if both $D$ and $k$ are fluctuating, and the magenta lines if $D$ and $k$ are fluctuating in a fully correlated way. In A, the current $j$ is imposed at $x=0$. In B, the concentration $c$ is imposed at $x=0$. Parameters are $\lambda/a = \sqrt{50}$, $\sigma_j/j_0 = \sigma_{c_0}/c_0 = 0$, $\sigma_D/D_0 = \sigma_k/k_0 = 0.1$. In the fully correlated case $2\rho_{D,k} = \rho_D \rho_k = (\alpha_D/D_0)^2 + (\alpha_k/k_0)^2$ while $\rho_{D,D}^k = 0$ otherwise. A Gaussian distribution was used for the noise terms in the numerical calculations. Steady states were calculated on a linear chain of size 100$a$. 
**Fig. S2. Relative uncertainty $\Sigma(x)$ of the steady state concentration $c(x)$ for the diffusion-degradation model with disorder in two dimensions.** The symbols indicate results from numerical calculations in which steady-state gradients were calculated for many (typically 100,000) realizations of the disorder. The lines show the corresponding analytical results for $\Sigma(x)$ that follow from (10). The blue lines show $\Sigma(x)$ if only $k$ is fluctuating, the red lines if both $D$ and $k$ are fluctuating, the magenta line if $D$ and $k$ are fluctuating in a fully correlated way, and the green lines if $D$, $k$ and the respective quantity imposed at the boundary at $x=0$ (j or $c_0$) are fluctuating. (A) Relative concentration uncertainty $\Sigma(x)$ with the current $j$ imposed at $x=0$. (B) $\Sigma(x)$ with the concentration $c_0$ imposed at $x=0$. (C) Like A, but with parameters corresponding to Fig. 2 of the main manuscript. (D) Relative concentration uncertainty $\Sigma(x)$ for the general case in which the hopping rates between two neighboring sites in opposite direction are uncorrelated. Current $j$ imposed at $x=0$. Compared to A-C, the magnitude of $\Sigma(x)$ is increased in this situation. Parameters as in Fig. S1, with $\sigma_j / j_0 = 0.1$ in A,B, $\sigma_j / j_0 = 0.037$ in C, $\sigma_j / j_0 = 0.25$ in D, and $\lambda / a = 7$ in C,D. A Gaussian distribution was used for the noise terms in the numerical calculations. Steady states were calculated on a simple cubic lattice of size $100a \times 100a$. 
Fig. S3. Relative concentration uncertainty $\Sigma(x)$ for the diffusion-degradation model with disorder for different space dimensionalities. All calculations were done with $j$ imposed at $x=0$. (A) Logarithmic plot of $\Sigma(x)$ in one dimension (red lines), in two dimensions (blue lines), and in three dimensions (green lines). For the solid lines, only $k$ is fluctuating and for the broken lines both $k$ and $j$ are fluctuating. Shown are the analytical results for $\Sigma(x)$ given by (8), (10) and (12) for the different space dimensionalities respectively. (B) Double-logarithmic plot of $\Sigma(x)$ for large $x$ in one and two dimensions. In these calculations, $k$ and $D$ are fluctuating. Numerical results are shown by symbols. In two dimensions, $\Sigma(x)$ was multiplied by a factor of five. For comparison, functions proportional to $x^{1/2}$ and $x^{1/4}$ are shown in red and blue, respectively. The inset shows the same data using linear axes. Parameters as in Fig. S1 with $\sigma_j / j_0 = 0.1$ and $\rho_D = 0$. Steady states in two dimensions were calculated on a simple cubic lattice of size $220a \times 100a$. 
Fig. S4. Relative concentration uncertainty $\tilde{\Sigma}(x)$ in presence of disk-to-disk variations of the current imposed at $x=0$. For the solid line $\sigma_j/j_0 = 0$, for the dashed line $\sigma_j/j_0 = 0.1$, and for the dotted line $\sigma_j/j_0 = 0.2$. Remaining parameters as in Fig. 2 of the main manuscript.
Fig. S5. Correlations between PMad and Dpp concentrations. Non-normalized PMad level of all nuclei shown in Fig. 5B of the main manuscript correlated with the non-normalized GFP-Dpp level at the same distance from the source in the same wing disk ($R=0.63$). Compare with Fig. 5C of the main manuscript, which shows the same plot for the normalized PMad data. These data were obtained from a set of $N=15$ wing disks from $dpp$ mutants rescued by a GFP-Dpp transgene using the UAS/Gal4 driver system.
I. THEORETICAL DESCRIPTION OF MORPHOGEN TRANSPORT IN A TISSUE WITH CELL-TO-CELL VARIABILITY

We introduce cell-to-cell variability as random components to the diffusion coefficient and the degradation rate in the diffusion-degradation equation which describes the time evolution of the morphogen concentration profile, see equation (1) in the experimental procedure of the main manuscript. This is done most naturally in a discrete description. We consider a lattice with sites corresponding to individual cells. In one dimension, the morphogen concentration on site \( n \) is denoted \( C_n \), with \( n = 0, 1, 2, \ldots \). Molecules are transported to neighboring sites with rates \( p_n^+ \) (from site \( n \) to \( n + 1 \)) and \( p_n^- \) (for the transport from \( n + 1 \) to \( n \)). In addition, molecules on site \( n \) are degraded with a rate \( k_n \). Cell-to-cell variability leads to variations of the rates \( p_n^\pm \) and \( k_n \) as a function of \( n \). To keep our discussion simple, we restrict ourselves to the simpler situation where \( p_n = p_n^+ = p_n^- \), i.e. transport in opposite directions between cells occurs at the same rate \( p_n \).

The concentrations \( C_n \) satisfy the kinetic equation

\[
\partial_t C_n = p_{n-1}(C_{n-1} - C_n) + p_n(C_{n+1} - C_n) - k_n C_n, \quad \text{for } n > 0,
\]

where \( \partial_t = \partial/\partial t \). The lattice begins at site \( n = 0 \) corresponding to the morphogen source. Two different boundary conditions are considered: fixed concentration \( C_0^0 \) and a morphogen source at \( n = 0 \) emitting morphogens at an imposed rate \( \nu \). The concentration \( C_0 \) then satisfies

\[
\partial_t C_0 = \nu + p_0(C_1 - C_0) - k_0 C_0.
\]

This discrete description can be generalized to square (or cubic) lattices in two and three dimensions (see Fig. 3 of the main manuscript).

In the absence of disorder (cell-to-cell variability) \( p = p_n \) and \( k = k_n \) are the same for all sites. On large scales, the concentrations follow a diffusion-degradation equation \( \partial_t c = D \nabla^2 c - kc \) with \( D = pa^2 \) and degradation rate \( k \). Here, \( c(x) = C_n \) with \( x = an \). Cell-to-cell variability corresponds to a situation where \( p_n = p + \eta_n \) and \( k_n = k + \zeta_n \). Here, \( \eta_n \) and \( \zeta_n \) are random variables with zero average. They are characterized by their correlators which we choose to be \( \langle \eta_n \eta_j \rangle = \sigma_D^2/a^4 \delta_{nj} \) and \( \langle \zeta_n \zeta_j \rangle = \sigma_k^2 \delta_{nj} \). Here, the brackets \( \langle \ldots \rangle \) denote an ensemble average over all realizations of the random variables. These relations imply that the values of \( \eta_n \) and \( \zeta_n \) at different bonds of the lattice are uncorrelated. The \( \eta_n \) and \( \zeta_n \) can
also be correlated at each lattice site: $\langle n_j \zeta_j \rangle = \rho_{kD}a^2\delta_{nj}$.

In addition to the rates $p_n$ and $k_n$, the rate of ligand influx into the system $\nu$ can be fluctuating, i.e. $\nu = \nu_0 + \chi$ where $\chi$ is a random variable with $\langle \chi \rangle = 0$, $\langle \chi^2 \rangle = \sigma^2_{\chi}/a^2$, and $\langle \chi n \rangle = \langle \chi \zeta \rangle = 0$ for all $n \geq 0$. In the case of a fixed concentration at $n = 0$, one can introduce fluctuations at the boundary very similarly: $C_0 = C_0^0 + \gamma$ with a random variable $\gamma$ satisfying $\langle \gamma \rangle = 0$, $\langle \gamma^2 \rangle = \sigma^2_{\gamma}$, and $\langle \gamma n \rangle = \langle \gamma \zeta \rangle = 0$. The standard deviations $\sigma_D/\sigma^2$, $\sigma_k$, $\sigma_j/\sigma$, and $\sigma_{n_0}$ of the noise terms $n$, $\zeta$, $\chi$, and $\gamma$ are assumed to be small compared to the mean values $p$, $k$, $\nu_0$, and $C_0^0$ respectively. Our discussion is mostly independent of the specific probability distributions of $n$, $\zeta$, $\chi$, and $\gamma$. It is only required that these distributions are tightly localized around their mean value zero.

## II. CONTINUUM LIMIT

In the presence of disorder, the kinetics of the concentration field can be described on large scales in a continuum limit. In $d$ dimensions, with $\vec{x}$ describing a position in space, i.e. $\vec{x} = (x, y)$ in $d = 2$ and $\vec{x} = (x, y, z)$ in $d = 3$, the concentration field $c(t, \vec{x})$ obeys

$$\partial_t c(t, \vec{x}) = \nabla \cdot [(D_0 + \eta(\vec{x})) \nabla c(t, \vec{x})] - (k_0 + \zeta(\vec{x})) c(t, \vec{x})$$  \hspace{1cm} (3)

Here $\eta(\vec{x})$ and $\zeta(\vec{x})$ denote noise terms with zero average and correlators $\langle \eta(\vec{x}) \eta(\vec{x}') \rangle = \sigma^2_D a^d \delta(\vec{x} - \vec{x}')$, $\langle \zeta(\vec{x}) \zeta(\vec{x}') \rangle = \sigma^2_{\chi} a^d \delta(\vec{x} - \vec{x}')$, and $\langle \eta(\vec{x}) \zeta(\vec{x}') \rangle = \rho_{kD} a^d \delta(\vec{x} - \vec{x}')$. These correlators express the continuum limits of the expressions introduced in the discrete case. The amplitude of the fluctuations of $D$ is $\sigma_D$ and accordingly $\sigma_k$ for $k$. A possible correlation of the fluctuations of $D$ and $k$ at a given position is measured by $\rho_{kD}$.

The fluctuations of the secretion rate of the source cells located at $x < 0$ are captured by imposing a current

$$(D_0 + \eta(\vec{x})) \partial_x c(\vec{x}, t) \big|_{x=0} = -j_0 - \chi(\vec{x}) \big|_{x=0}$$ \hspace{1cm} (4)

across the boundary surface at $x = 0$, where $\chi(\vec{x})$ is a noise term with $\langle \chi(\vec{x}) \chi(\vec{x}') \rangle_{x=0} = \sigma^2_{\chi} a^{(d-1)} \delta^{(d-1)}(\vec{x} - \vec{x}')|_{x=0}$.

### A. Effects of disorder on steady state gradients

The steady state solutions $c(\vec{x})$ of (3) depend on the particular realization of the disorder, reflecting the effects of cell-to-cell variability. The average gradient $\bar{c}(x) = \langle c(\vec{x}) \rangle$ is given by
an ensemble average over all possible realizations of the disorder. Alternatively, in a two-
dimensional geometry with a line source at $x = 0$, the average gradient can be determined
by averaging along the $y$ direction for given $x$ in a single realization of the disorder.

We first discuss the problem in $d = 1$. It is assumed that the amplitude of the noise is
small, i.e. $\sigma_D/D_0 \ll 1$ and $\sigma_k/k_0 \ll 1$. We calculate the variance of the concentration

$$\sigma_c^2(x) = \langle (c(x) - \bar{c}(x))^2 \rangle$$

by using a perturbation expansion to first order in the small parameters $\sigma_D/D_0$ and $\sigma_k/k_0$.

Note that to first order the average concentration is given by $\bar{c}(x) = c_0 e^{-x/\lambda}$ where $\lambda = \sqrt{D_0/k_0}$ is the diffusion length and $c_0 = j_0/\sqrt{k_0D_0}$.

The results of this calculation can be expressed in terms of Green’s functions $G(x, x')$ of
the linear operator $(D_0\partial_x^2 - k_0)$ which satisfy $(D_0\partial_x^2 - k_0)G(x, x') = \delta(x-x')$. To satisfy the
two different boundary conditions at $x = 0$, two Green’s functions $G_+(x, x')$ with $G_-(0, x') = 0$ and $\partial_xG_+(x, x')|_{x=0} = 0$ respectively are needed. In one dimension these functions are given by

$$G_\pm(x, x') = \frac{-1}{2\sqrt{k_0D_0}} \left( e^{-|x-x'|/\lambda} \pm e^{-(x+x')/\lambda} \right).$$

To first order in our perturbation expansion, the variance of the concentration is given by

$$\langle \sigma_c^2(x) \rangle^2 = D_0^2 \left( \partial_x G_\pm(x, x') \right|_{x'=0}^2 \right)^2 \sigma_0^2 + G_\pm(x, 0)^2 \sigma_j^2$$

$$+ a \int_0^\infty dx' \left( \sigma_0^2 \beta'(x')^2 \right) \left( \partial_x G_\pm(x, x')^2 + \sigma_k^2 \right)^2 + 2\lambda D_0 G_\pm(x, x') \beta(x') \beta'(x') \partial_x G_\pm(x, x').$$

Here, we use a condensed notation for both choices of the boundary condition at $x = 0$: $\sigma_c^+$ denotes the solution for a fixed current and $\sigma_c^-$ the solution for a fixed concentration at $x = 0$. Using the explicit expressions for the Green’s functions and $\bar{c}(x)$, this integral can be solved and expressed in terms of elementary functions. As discussed in the main text, a dimensionless measure of the relative concentration uncertainty at $x$ is

$$\Sigma(x) = \frac{\langle (c(x) - \bar{c}(x))^2 \rangle^{1/2}}{\bar{c}(x)} = \frac{\langle \sigma_c(x)^2 \rangle^{1/2}}{\bar{c}(x)}.$$
\[ \Sigma^\pm_B(x)^2 = \left( \frac{\sigma_D}{\lambda_0} \right)^2 \]
\[ \Sigma_{\Gamma B}(x)^2 = \left( \frac{\sigma_D}{\lambda_0} \right)^2 \]
\[ \Sigma^+_k(x)^2 = \frac{a}{8\lambda} \left( \frac{\sigma_k}{k_0} \right)^2 \left( 1 \pm 2 \mp e^{-2x/\lambda} + \frac{2x}{\lambda} \right) \]
\[ \Sigma^+_D(x)^2 = \frac{a}{8\lambda} \left( \frac{\sigma_D}{D_0} \right)^2 \left( 1 \pm 2 \mp 3e^{-2x/\lambda} + \frac{2x}{\lambda} \right) \]
\[ \Sigma^+_{kD}(x) = \frac{a}{4\lambda} \frac{\rho_{kD}}{k_0 D_0} \left( 1 \pm e^{-2x/\lambda} - \frac{2x}{\lambda} \right). \] (8)

As the relative concentration fluctuations become arbitrarily large for large \( x \), these results are only valid in a finite region \( 0 \leq x \leq M \) for some \( M > 0 \).

The steady state of (3) for \( d = 2 \) can be calculated iteratively as in the one dimensional situation. The free Green’s function for the operator \( (D_0(\partial_x^2 + \partial_y^2) - K_0)G_0(\bar{x}, \bar{x}') = \delta(\bar{x} - \bar{x}') \) is

\[ G_0(\bar{x}, \bar{x}') = \frac{-1}{2\pi D_0} K_0(|\bar{x} - \bar{x}'|/\lambda), \]

where \( K_0 \) is a modified Bessel function of the second kind [1]. Using a mirror image technique, one can construct Green’s functions \( G_{\pm}(\bar{x}, \bar{x}') \) that satisfy \( G_{-}(\bar{x}, \bar{x}') |_{x=0} = 0 \) and \( \partial_x G_{+}(\bar{x}, \bar{x}') |_{x=0} = 0 \) respectively:

\[ G_{\pm}(x, y, x', y') = G_0(x, y, x', y') \pm G_0(x, y, -x', y'). \] (9)

To first order, the variance of \( c(\bar{x}) \) is

\[ \langle \sigma_c^2(\bar{x})^2 \rangle = a \int_{-\infty}^{\infty} dy' \left( \sigma_c^2 D_0 \left( \partial_x G_{\pm}(\bar{x}, \bar{x}') \right|_{x'=0} \right)^2 + \sigma_J^2 G_\pm(x, y, 0, y')^2 \]
\[ + a^2 \int_{0}^{\infty} dx' \int_{-\infty}^{\infty} dy' \left( \frac{\sigma_k^2 G_{\pm}(\bar{x}, \bar{x}')}{\lambda} c(x')^2 + \sigma_D^2 c'(x')^2 (\partial_x G_{\pm}(\bar{x}, \bar{x}'))^2 \right) \]
\[ + 2\rho_{kD} c(x') c'(x') G_{\pm}(\bar{x}, \bar{x}') \partial_x G_{\pm}(\bar{x}, \bar{x}'). \] (10)

The resulting relative concentration uncertainty grows asymptotically as \( \Sigma(x) = \langle \sigma_c(\bar{x})^2 \rangle^{1/2} / c(\bar{x}) \sim x^{1/4} \). The first term in (10) is due to the fluctuations of the current across the boundary line at \( x = 0 \) or the concentration that is fixed there. This term alone decreases as \( \Sigma(x) \sim x^{-1/4} \) for large \( x \). Positive correlations between the fluctuations of \( k_0 \) and \( D_0 \) increase the precision as in the one dimensional case.

One can calculate the standard deviation of the concentration in \( d = 3 \) as well. We are interested in the steady state solution of (3) with \( \bar{x} = (x, y, z) \) and \( \nabla = (\partial_x, \partial_y, \partial_z) \) in the
half-space $x \geq 0$. Either the concentration or the current is imposed on the boundary plane $x = 0$, i.e. $c(x)|_{x=0} = c_0 + \gamma(y,z)$ or $\partial_x c(x)|_{x=0} = -D_0^{-1}(j_0 + \chi(y,z))$.

The Green’s functions for the two boundary conditions at $x = 0$ can again be constructed:

$$G_{\pm}(\vec{x},\vec{x'}) = \frac{-1}{4\pi D_0} \left( \frac{e^{-r/\lambda}}{r} \pm \frac{e^{-r_m/\lambda}}{r_m} \right),$$

with $r = ((x - x')^2 + (y - y')^2 + (z - z')^2)^{1/2}$ and $r_m = ((x + x')^2 + (y - y')^2 + (z - z')^2)^{1/2}$.

The result for the variance of $c(\vec{x})$ to first order in perturbation theory is

$$\langle \sigma^2_c(\vec{x}) \rangle = a^2 \int_{-\infty}^{\infty} dy' \int_{-\infty}^{\infty} dz' \left( \sigma_{\alpha 0}^2 D_0^2 (\partial_{\alpha'} G_{\pm}(\vec{x},\vec{x'}))^2 + \sigma_j^2 G_{\pm}(\vec{x},\vec{x'}))^2 \right) |_{x'=0}$$

$$+ a^3 \int_0^x \int_{-\infty}^{\infty} dx'' \int_{-\infty}^{\infty} dy'' \int_{-\infty}^{\infty} dz'' \left( \sigma_k^2 G_{\pm}(\vec{x},\vec{x'}) c(x'')^2 + \sigma_j^2 \partial_{\alpha'}(x'') \sigma_j^2 G_{\pm}(\vec{x},\vec{x'}) \right)$$

$$+ 2 \rho_{kD} c(x') \partial_{\alpha'}(x'') \partial_{\alpha''} G_{\pm}(\vec{x},\vec{x'}) |_{x'=0},$$

(12)

We have integrated (12) numerically. The resulting relative concentration uncertainty $\Sigma(x)$ is shown in Suppl. Fig. 3 A for a fixed current at the boundary. Asymptotically, $\Sigma(x) \sim \ln(x)$. The contribution from the boundary term alone decreases asymptotically as $\Sigma(x) \sim x^{-1/2}$.

**B. Effects of disk-to-disk variations of the morphogen secretion rate**

As discussed in the main text, the total fluorescence intensity (FI) of the non-normalized GFP-Dpp FI profiles measured experimentally varies considerably from disk-to-disk. This is most likely due to variations in the secretion rate of morphogens from the source cells between wing disks from different larvae.

Such disk-to-disk variations can easily be included in our theoretical description. In addition to the cell-to-cell fluctuations which are already taken into account in (4), we assume that the current imposed at $x = 0$ fluctuates with a standard deviation $\sigma_{j0}$ about its mean value $j_0^0$ for different gradients in our ensemble. We further assume that these fluctuations are not correlated with any of the cell-to-cell fluctuations in the system. The relative concentration uncertainty $\tilde{\Sigma}(x)$ that takes disk-to-disk variations of the morphogen secretion rate into account is then

$$\tilde{\Sigma}(x) = \sqrt{(\sigma_{j0}/j_0^0)^2 + \Sigma(x)^2},$$

(13)

where $\Sigma(x)$ is the relative concentration uncertainty in the absence of disk-to-disk variations of the morphogen secretion rate which was calculated above. In Suppl. Fig. 4, we show
$\tilde{\Sigma}(x)$ for different values of $\sigma_{j_0}$. While the behavior of $\tilde{\Sigma}(x)$ is qualitatively the same as that of $\Sigma(x)$, the minimum of $\tilde{\Sigma}(x)$ is less and less pronounced in relative terms for increasing values of $\sigma_{j_0}$.

III. NUMERICAL SIMULATIONS

We have performed numerical calculations of the discrete description (1) for the two different boundary conditions at $x = 0$ in one and two dimensions. At the remaining boundaries, we imposed zero flux boundary conditions. A large number of steady state gradients was calculated for different realizations of the disorder using a Gaussian distribution for the random variables. From these, the average value and standard deviation of $C_n$ at all lattice sites $n$ were calculated. The resulting relative concentration uncertainty is shown in Suppl. Fig. 1 for the different boundary conditions in $d = 1$ and in Suppl. Fig. 2 for $d = 2$. A good agreement with the results of the perturbative calculation is found.

Furthermore, we have numerically calculated the relative concentration uncertainty $\Sigma(x)$ in the general case in which the rates of transfer in opposite directions between neighboring sites are uncorrelated. In one dimension this implies $p_n^+ \neq p_n^-$ (Fig. 1C of the main manuscript). Suppl. Fig. 2D shows that while the qualitative features of $\Sigma(x)$ remain the same in this situation, the uncertainty is about an order of magnitude larger than in the case $p_n^+ = p_n^-$ for the same noise amplitude $\sigma_D/D_0 = 0.1$. This implies that the values of $\Sigma(x)$ are comparable to those observed experimentally.

Table S1. Average values and variability of the key quantities discussed in the main text

<table>
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<th>Quantity</th>
<th>Mean value [μm]</th>
<th>Standard deviation [μm]</th>
<th>Variation coefficient</th>
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<td>0.26</td>
</tr>
<tr>
<td>PMad decay length $\lambda^{\text{Mad}}$</td>
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<td>0.18</td>
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<td>Sal range $x^*$</td>
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<td>0.16</td>
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<tr>
<td>Wing disk size $L$</td>
<td>132.6</td>
<td>21.0</td>
<td>0.16</td>
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</table>

These results were obtained from a set of $N=15$ wing disks from dpp mutants rescued by a GFP-Dpp transgene using the UAS/Gal4 driver system.
Table S2. Correlation indices $R$ of the key quantities discussed in the main text

<table>
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<th></th>
<th>$\lambda^{\text{pmin}}$</th>
<th>$\lambda^{\text{pmax}}$</th>
<th>$x^*$</th>
<th>$L$</th>
<th>$r_{\text{pmad}}$</th>
</tr>
</thead>
<tbody>
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<td>$x^*$</td>
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<td>0.49</td>
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<tr>
<td>$L$</td>
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<td>0.03</td>
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<tr>
<td>$r_{\text{pmad}}$</td>
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<td>0.30</td>
<td>0.26</td>
<td>0.58</td>
<td>0.55</td>
</tr>
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</table>

The strongest correlations are observed between the disk size $L$ and Sal range $x^*$, the total PMad level $r_{\text{pmad}}$ and $x^*$ and between $r_{\text{pmad}}$ and $L$. These results were obtained from a set of $N=15$ wing disks from dpp mutants rescued by a GFP-Dpp transgene using the UAS/Gal4 driver system.