



Ancestral Developmental Potential Facilitates Parallel Evolution in Ants

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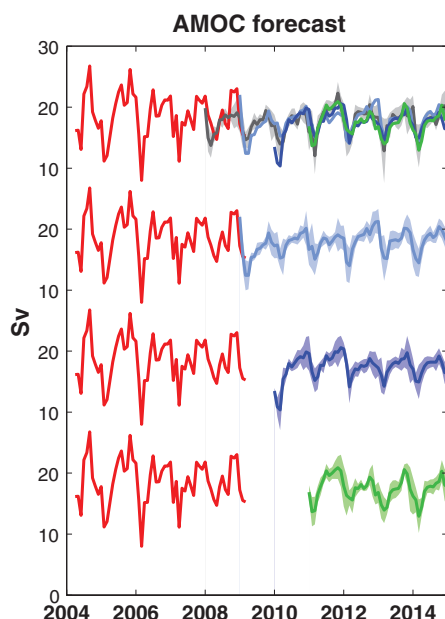


Fig. 4. Multiyear predictions of AMOC transport. RAPID/MOCHA time series are shown in red; ensemble mean forecasts are shown in dark gray, light blue, dark blue, and green for the forecasts starting in January 2008, January 2009, January 2010, and January 2011, respectively. The pale shading represents the 95% confidence intervals of the nine-member forecast ensemble initialized in January 2008, January 2009, January 2010, and January 2011.

not—is inevitable as long as in situ ocean interior measurements cannot be made in real time.

For all start years, the ensemble-mean forecasts until 2014 indicate a generally stable AMOC (Fig. 4). However, the forecast initialized in March 2010 shows a pronounced AMOC minimum in March 2010 that arises from a minimum in EK (fig. S7),

which in turn is induced by an extremely negative North Atlantic Oscillation in winter 2009–2010 (28). The real AMOC minimum in March 2010 may turn out to be even deeper than predicted, because our ensemble mean underpredicts AMOC amplitude (fig. S2). We are confident, however, that the AMOC minimum in March 2010 will be a short-lived phenomenon; our confidence is based on the insensitivity of our AMOC and MO forecasts to the start year.

We cannot readily generalize our results for 26.5°N to other latitudes; recent studies reported a change in the character of AMOC fluctuations around 40°N, with a strong decadal component to the north and enhanced higher-frequency variability to the south (29–31). However, for 26.5°N, we have established AMOC hindcast skill, we understand that this skill arises from the mid-ocean transport, and we confidently predict a stable AMOC at least until the end of 2014. Moreover, our findings demonstrate that skill in climate prediction arises not only from the large ocean thermal inertia but potentially also from the long time scales of internal ocean dynamics.

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Supporting Online Material

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Ancestral Developmental Potential Facilitates Parallel Evolution in Ants

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Complex worker caste systems have contributed to the evolutionary success of advanced ant societies; however, little is known about the developmental processes underlying their origin and evolution. We combined hormonal manipulation, gene expression, and phylogenetic analyses with field observations to understand how novel worker subcastes evolve. We uncovered an ancestral developmental potential to produce a “supersoldier” subcaste that has been actualized at least two times independently in the hyperdiverse ant genus *Pheidole*. This potential has been retained and can be environmentally induced throughout the genus. Therefore, the retention and induction of this potential have facilitated the parallel evolution of supersoldiers through a process known as genetic accommodation. The recurrent induction of ancestral developmental potential may facilitate the adaptive and parallel evolution of phenotypes.

The wingless worker caste, a universal feature of ants (1, 2), has repeatedly expanded into a complex system of morphologi-

cal and behavioral subcastes. The existence of these subcastes has long fascinated biologists (3–9), yet little is known about their develop-

mental and evolutionary origin (7, 8). The ant genus *Pheidole* is one of the most species-rich genera, with 1100 species worldwide (10, 11). All *Pheidole* species have two worker subcastes: minor workers (Fig. 1C) that perform most tasks in the nest and forage and soldiers (Fig. 1B) that

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defend the nest and process food (11). This complex worker caste system is thought to have promoted the remarkable diversification of *Pheidole* by enhancing the division of labor (11).

In a wild *P. morrisi* colony, we discovered several anomalous soldier-like individuals. These individuals are anomalous because they are significantly larger than normal soldiers (Fig. 2, A and B, and fig. S1), and unlike normal soldiers, they have mesothoracic wing vestiges (Fig. 2, C and D) and rarely occur in nature. These anomalous soldiers are similar to a supersoldier subcaste, which is known to be continually produced in eight *Pheidole* species (fig. S2) (10–12). These species co-occur with army ants and live exclusively in the deserts of the American southwest and northern Mexico (11). In one of these species, *P. obtusospinosa* (Fig. 2, E and I), a major function of the supersoldier subcaste is to block the nest entrance with their extra-large heads and engage in combat to defend against army ant raids (13).

The similarity between the supersoldier-like anomalies in *P. morrisi* and the supersoldier subcaste suggests that they share a developmental origin. Normal soldier development in *Pheidole* may provide insight into how supersoldier-like anomalies may have originated. The soldier subcaste is determined late in larval development at a soldier–minor worker switch point (Fig. 1), which is largely controlled by nutrition (5) and mediated by juvenile hormone (JH) (14, 15). Soldier development is defined by two features: (i) Soldier-determined larvae grow larger than minor worker larvae; and (ii) they develop a pair of vestigial forewing discs in their mesothoracic segment (Fig. 1, E and F) (14–16). These discs show a soldier-specific expression of *spalt* (*sal*) (Fig. 1E) (1), a key gene in the network underlying wing polyphenism in *Pheidole*. *Sal* is a key gene because its expression is spatiotemporally associated with the induction of apoptosis in these vestigial forewing discs (17, 18). Therefore, the supersoldier-like anomalies we found in *P. morrisi* were likely to have originated from the abnormal growth of soldier larvae and their vestigial wing discs. Based on this insight, we predicted that the evolution of the supersoldier subcaste in *Pheidole* occurred through developmental changes that elaborated these two features.

We tested this prediction in *P. obtusospinosa* and *P. rhea*, two species that have a supersoldier subcaste (11). As predicted, their supersoldier larvae grow larger (Fig. 2, F and J, and fig. S3, B and F) and develop two pairs of large vestigial wing discs relative to their soldier larvae (Fig. 2, G and K, and fig. S3, C and G). Furthermore, vestigial wing discs in supersoldier larvae show an elaborated pattern of *sal* expression in the wing pouch relative to those of soldier larvae (Fig. 2, H and L, and fig. S3, D and H, black arrows). We then resolved the evolutionary history of their supersoldier subcaste by reconstructing a phylogeny of 11 *Pheidole* species (fig. S5). Of these, only *P. obtusospinosa* and *P. rhea* have a supersol-

dier subcaste. Our phylogenetic analysis suggests that the supersoldier subcaste has evolved independently, because *P. rhea* is one of the most basal species of this genus, whereas *P. obtusospinosa* is derived (fig. S5) (10). Therefore, the supersoldier subcaste has evolved in parallel, because similar developmental changes underlie its inde-

pendent evolution in *P. obtusospinosa* and *P. rhea*. Furthermore, our phylogenetic analysis suggests that, relative to *P. obtusospinosa*, there are six basal and four derived species (fig. S5). We found that soldier larvae of these basal and derived species differ in their vestigial wing disc number and wing pouch expression of *sal* (fig. S6). This indi-

Fig. 1. Wing polyphenism in *P. morrisi*: the ability of a single genome to produce (A) winged queens and wingless (B) soldiers and (C) minor workers (2). Caste determination occurs at two JH-mediated switch points in response to environmental cues (1, 15, 30). (D) Wing discs in queen larvae showing conserved hinge and pouch expression of *sal*. (E) Vestigial wing discs in soldier larvae showing a soldier-specific pattern of *sal* expression, where it is conserved in the hinge but down-regulated in the pouch. Asterisks represent the absence of visible wing discs and *sal* expression in (E) soldier and (F) minor worker larvae. Scale bars indicate the relative sizes of queen, soldier, and minor worker larvae and adults.

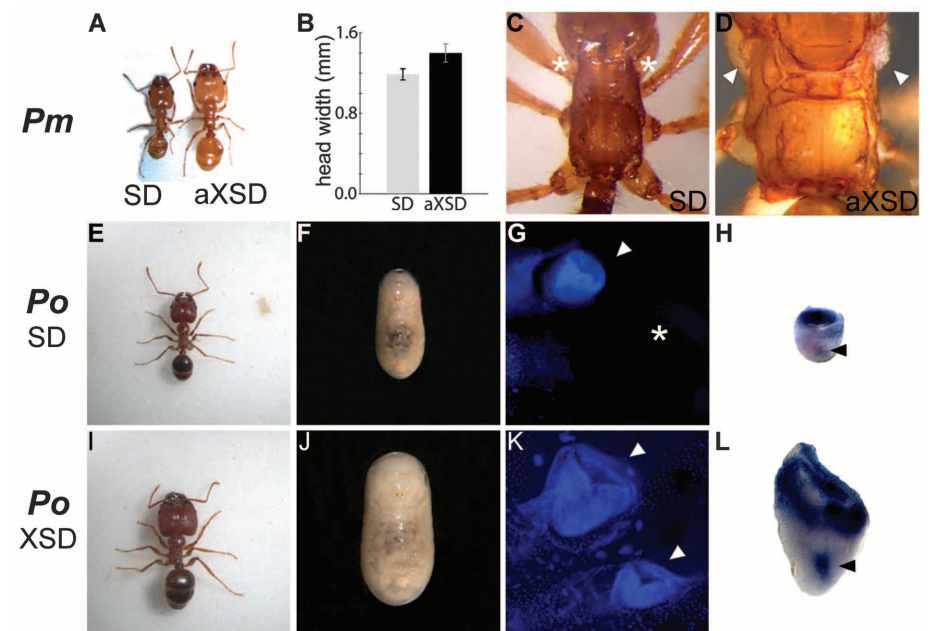
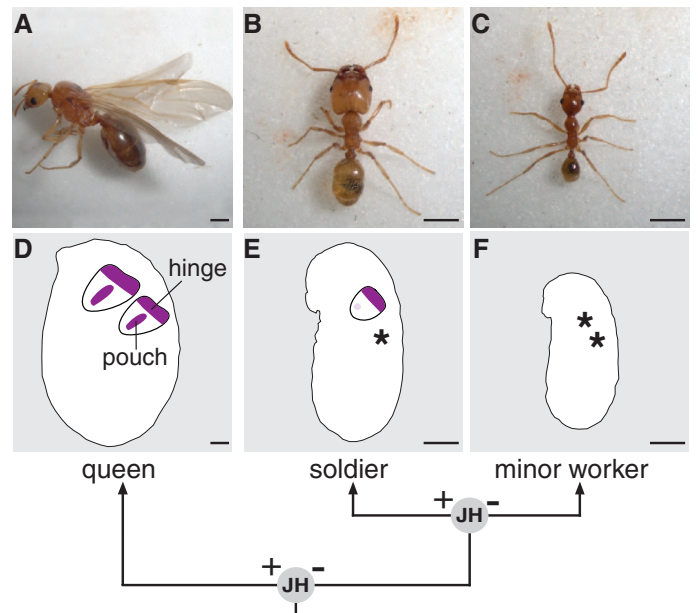


Fig. 2. Comparison of *P. morrisi* (Pm) ants: (A, left) Normal adult soldier (SD) and (A, right) anomalous supersoldier (aXSD). (B) Mean and standard deviation of head width of normal SD (gray) and aXSD (black) (fig. S1), and thorax of (C) a normal SD and (D) an aXSD. Comparison of *P. obtusospinosa* (Po) ants: adults of (E) SD and (I) supersoldier (XSD); larvae of (F) SD and (J) XSD; and vestigial wing discs [stained with 4',6'-diamidino-2-phenylindole (DAPI)] and *sal* expression in SD (G and H and fig. S4A) and XSD (K and L and fig. S4B). White arrowheads indicate the presence of mesothoracic vestigial wing buds or discs; asterisks denote their absence. Black arrowheads indicate *sal* expression in the wing pouch. Adult, larval, and vestigial wing disc images are all to scale. See fig. S3 for a comparison of *P. rhea* SD and XSD.

cates that the supersoldier subcaste has evolved in parallel despite the evolutionary divergence of soldier development.

Application of methoprene (a JH analog) to *Pheidole* larvae has been shown to induce the development of unusually large soldier pupae (15). In *P. morrisi*, we found that methoprene can induce the development of larvae and adults that mimic the anomalous supersoldier-like individuals of *P. morrisi* and the supersoldiers of *P. obtusospinosa* and *P. rhea*. First, induced

supersoldier larvae (Fig. 3G) and adults (Fig. 3B) are significantly larger than untreated controls (Fig. 3, D and A, and fig. S7), and several of the induced adult supersoldiers have mesothoracic wing vestiges (Fig. 3C). Second, the relative size ranges of induced supersoldiers overlap with those of anomalous and naturally produced supersoldiers (fig. S8). Finally, we found vestigial wing discs of induced supersoldier larvae (Fig. 3, H and I, and fig. S9, B to D and F to H) that mimic those of supersoldier larvae in *P. obtusospinosa* (Fig. 2,

K and L) and *P. rhea* (fig. S3, G and H). Therefore, although *P. morrisi* lacks a supersoldier subcaste, there is a developmental potential to produce supersoldiers that can be induced through JH. Furthermore, the occurrence of supersoldier-like anomalies in *P. morrisi* (Fig. 2A) and other *Pheidole* species (16) suggests that this potential is recurrently induced in nature. This recurrent induction, which is probably mediated by JH, may be caused by nutrition, because it has been shown that environmental variation in nutrition (3) and experimentally increasing nutrition (5) produces supersoldier-like anomalies in *Pheidole* colonies.

We discovered that this developmental potential to produce supersoldiers can be induced by methoprene in other derived (*P. hyatti*) and basal (*P. spadonia*) *Pheidole* species that lack a supersoldier subcaste. As in *P. morrisi*, we found vestigial wing discs of induced supersoldier larvae in *P. hyatti* (fig. S9, J and N) and *P. spadonia* (fig. S9, R and V) that mimic those of supersoldier larvae in *P. obtusospinosa* (Fig. 2, K and L) and *P. rhea* (fig. S3, G and H). Therefore, the developmental potential to produce supersoldiers has been retained and was probably present in the common ancestor of all *Pheidole* (Fig. 4). Without a priori knowledge of this ancestral developmental potential, we would have inferred that the supersoldier subcaste has evolved de novo: once in *P. rhea* and once in *P. obtusospinosa* (fig. S5) (10). However, our results support an alternative explanation for the parallel evolution of supersoldiers: The developmental potential and phenotypic expression of a novel supersoldier subcaste originated in the common ancestor of all *Pheidole* (Fig. 4, section i); the phenotypic expression of supersoldiers was subsequently lost, but the ancestral potential to produce them was retained (Fig. 4, section ii); and this potential was then actualized in *P. obtusospinosa*, leading to the re-evolution of a supersoldier subcaste (Fig. 4, section iii).

Finally, we showed that this ancestral potential was actualized in *P. obtusospinosa* through the re-evolution of a second JH-sensitive period mediating a soldier-supersoldier switch point (fig. S10). We applied methoprene to larvae that had passed the soldier–minor worker switch point but whose caste fate as either soldiers or supersoldiers was still undetermined. We found that applying methoprene to these larvae induced the development of a significantly greater proportion of supersoldiers (fig. S11). Collectively, our results indicate that the supersoldier subcaste in *P. obtusospinosa* re-evolved through genetic accommodation. This process occurs when: (i) a novel phenotype is induced and (ii) this phenotype is incorporated into the population through selection on genes that control its frequency and form of expression (19, 20). Environmental induction of the ancestral potential may have recurrently produced supersoldier-like anomalies in *P. obtusospinosa*. These anomalies would persist, because colonies of *Pheidole* generally care for and buffer anomalies against purifying

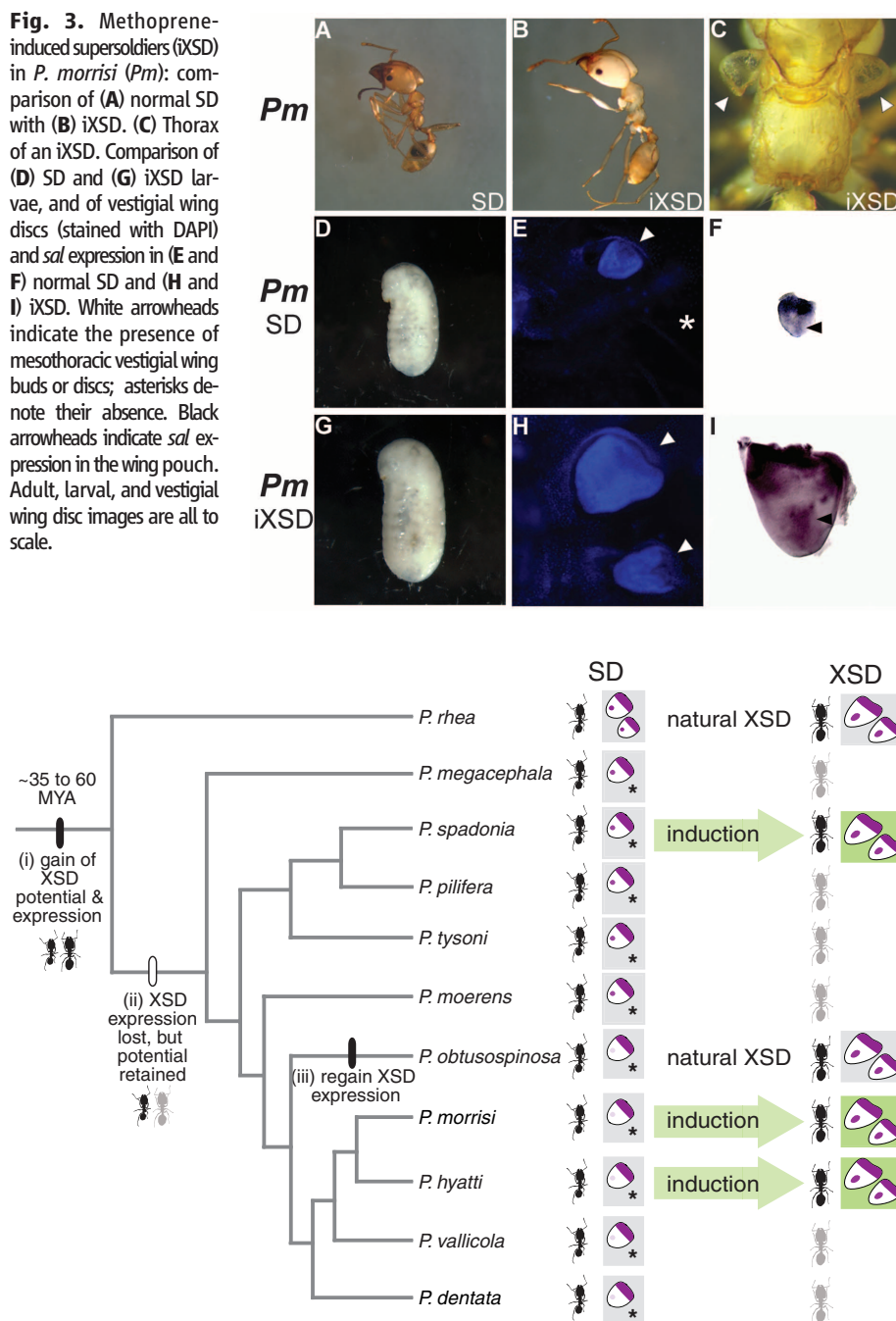


Fig. 4. Evolutionary history of ancestral developmental potential and phenotypic expression of supersoldiers (XSDs). MYA, million years ago. Purple represents the pattern of *sal* expression; asterisks indicate the absence of vestigial wing discs and *sal* expression. Green arrows and boxes represent the induction of XSD potential.

selection (3). Selection on *P. obtusospinosa* colonies may have incorporated induced supersoldier-like anomalies by increasing their frequency through modification of the JH system (fig. S12) and by inhibiting the formation of any wing vestiges (fig. S13 and S14). Army ant raids may have been a selective pressure that incorporated these anomalies, because *P. obtusospinosa* supersoldiers currently use their extra-large heads to defend against these raids (13).

Selection for re-evolving supersoldiers may generally be reduced, because almost all *Pheidole* species lack a supersoldier subcaste (10, 11). *P. hyatti* provides insight into how this selective pressure can be reduced: Although *P. hyatti* retains the developmental potential (Fig. 4) and lives in an ecological environment similar to that of *P. obtusospinosa*, it has not re-evolved a supersoldier subcaste (11). Instead, *P. hyatti* uses nest evacuation behavior when attacked by army ants (21). The retention of this potential in *P. hyatti* and other *Pheidole* species that lack a supersoldier subcaste may therefore be due to a clade-specific constraint (22). This constraint may have arisen from having the same hormone (JH) mediate the determination of both soldiers and supersoldiers in the common ancestor of all *Pheidole*. Soldiers and supersoldiers are both defined by their larval size and the development of their vestigial wing discs, which indicates that their developmental programs share many modules. Therefore, the ancestral potential to produce supersoldiers cannot be lost without compromising the developmental program of soldiers.

Recurrent phenotypes reflecting ancestral potentials have long been recognized as widespread in plants and animals (6, 19, 23–28). Because of the lack of empirical evidence, however, the evolutionary significance of these recurrent phenotypes has been underappreciated (19, 29). We uncovered an ancestral developmental potential to produce a novel supersoldier subcaste that has been retained throughout a hyperdiverse ant genus that evolved ~35 to 60 million years ago (10) (Fig. 4). Our results suggest that the recurrent induction of ancestral developmental potential is an important source of adaptive variation for selection that facilitates the adaptive and parallel evolution of novel phenotypes.

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Supporting Online Material

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Fitness Trade-Offs and Environmentally Induced Mutation Buffering in Isogenic *C. elegans*

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Mutations often have consequences that vary across individuals. Here, we show that the stimulation of a stress response can reduce mutation penetrance in *Caenorhabditis elegans*. Moreover, this induced mutation buffering varies across isogenic individuals because of interindividual differences in stress signaling. This variation has important consequences in wild-type animals, producing some individuals with higher stress resistance but lower reproductive fitness and other individuals with lower stress resistance and higher reproductive fitness. This may be beneficial in an unpredictable environment, acting as a “bet-hedging” strategy to diversify risk. These results illustrate how transient environmental stimuli can induce protection against mutations, how environmental responses can underlie variable mutation buffering, and how a fitness trade-off may make variation in stress signaling advantageous.

A specific mutation can have different consequences in different individuals. For example, even in “Mendelian” human diseases, such as cystic fibrosis, an inherited mutation can result in severe disease in one individual but a milder phenotype in another (1). Incomplete penetrance is also observed in isogenic model organisms and is poorly understood (2–4).

Many mutations have outcomes that depend on the activity of molecular chaperones—

proteins that aid the folding of other macromolecules (5–14). More generally, molecular mechanisms that promote environmental robustness (survival after environmental challenges) also tend to increase mutational robustness [the extent to which an organism’s phenotype remains constant in spite of mutation (15–17)].

We investigated whether genetically increasing environmental stress resistance could modify mutation penetrance in the model organism

Caenorhabditis elegans. We used a transgene to overexpress the transcription factor heat shock factor 1 (HSF-1), a master regulator of the environmental stress response. Transgenic animals are more resistant to a range of environmental challenges (18, 19) and show a delayed age-dependent reduction in protein-folding homeostasis (20). We crossed the *hsf-1* transgenic animals with strains carrying diverse mutations that affect development but with outcomes that vary across individuals (table S1).

In 8 out of 11 tested cases, mutation penetrance was reduced in the transgenic animals (Fig. 1, fig. S1, and table S2). Protection was observed for mutations affecting both embryonic (Fig. 1A) and postembryonic (Fig. 1B) development. For example, embryonic lethality caused by a deletion in the intermediate filament protein gene *ifb-1* reduced from 33% to 17% (48% of animals that would have died were protected, $P = 5.7 \times 10^{-12}$) (Fig. 1, fig. S1, and table S4). The buffered mutations are molecularly diverse and act in distinct

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