

# Prairie Dogs Disperse When All Close Kin Have Disappeared

John L. Hoogland

Because competition decreases inclusive fitness among kin, Hamilton and May predicted that the presence of nearby kin should induce the dispersal of individuals from the natal territory, independent of pressures to avoid inbreeding. Many studies support this landmark prediction, but research over 31 years with prairie dogs reveals the opposite pattern: Young females are 12.5 times more likely to disperse in the absence of mother and siblings for one species, and 5.5 times more likely for another species. Such striking patterns probably occur because cooperation among kin is more important than competition among kin for young prairie dogs. The inability to cooperate with close kin, due to their absence, prompts a search for a new territory where cooperation might be less crucial for survival and reproduction.

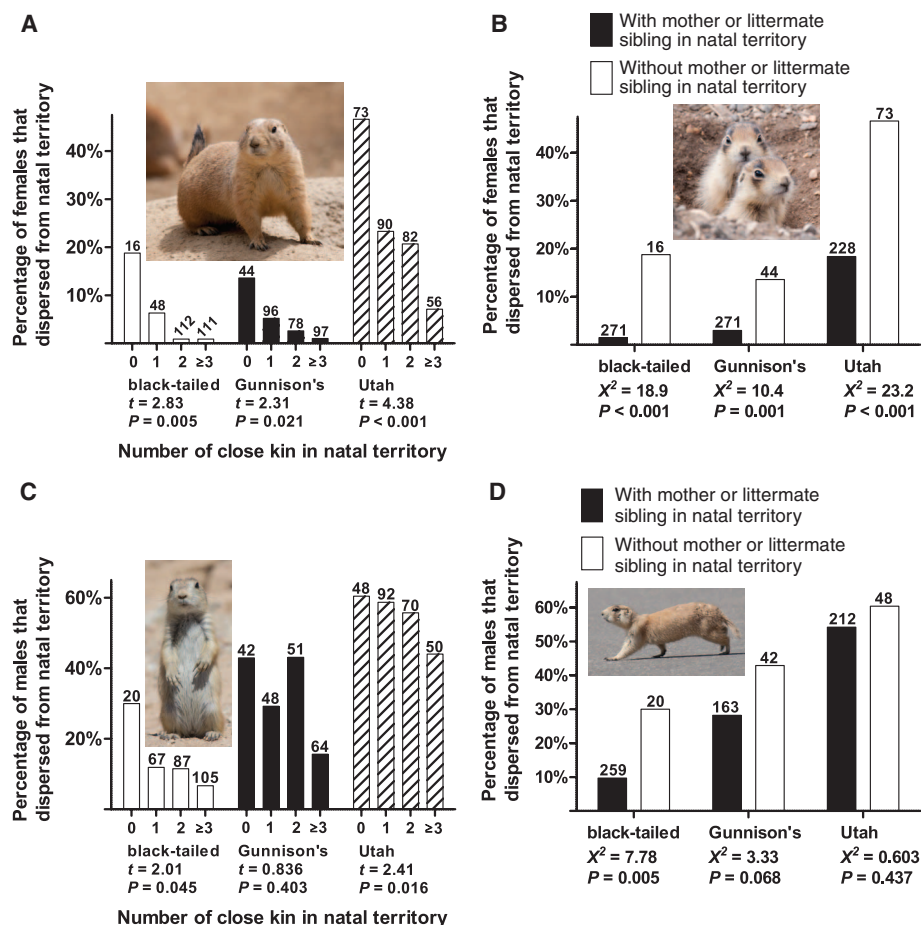
Natal dispersal, the emigration from an individual's territory of birth, has important consequences for demography, gene flow, range expansion, conservation, and population dynamics (1–8). Natal dispersal occurs in plants and animals across all taxa, but the identification of factors that drive dispersal has nonetheless been difficult (1, 2, 5). Because kin within the natal territory compete for resources, Hamilton and May (9) predicted that the presence of nearby kin should induce natal dispersal, irrespective of attempts to avoid inbreeding. When kin of the natal territory engage in cooperative behaviors (10–12), however, the benefits of cooperation might outweigh the costs of competition; if so, then the absence of kin might induce natal dispersal (3–8, 10–13). Studies of several diverse species support Hamilton and May's (9) seminal prediction that the presence of nearby kin induces natal dispersal (14–16), but data for the shaping of natal dispersal by cooperation among kin are scarce. In field research spanning 31 years, I investigated the effect of nearby kin on natal philopatry (i.e., remaining in the natal territory) and natal dispersal of prairie dogs of three species that inhabit grassland ecosystems of the western United States: black-tailed (*Cynomys ludovicianus*, from 1975 to 1988), Gunnison's (*C. gunnisoni*, from 1989 to 1995), and Utah (*C. parvidens*, from 1996 to 2005) (17–20).

Prairie dogs are large (300 to 900 g for adults, which are  $\geq 1$  year old), colonial, diurnal, burrowing, herbivorous rodents of the squirrel family (Sciuridae) (17–20). Colonies of all three species contain territorial, contiguous family groups called clans, which typically contain one sexually mature male, two to five sexually mature females, and one or two sexually immature yearling males (17–20). Prairie dogs are excellent models for a study of natal dispersal because they are easy to live-trap, mark, and observe, and because dispersers usually move only short distances to nearby territories (17–21). My results come from the tracking of wild prairie dogs living under natural

conditions, including all 2036 female offspring and all 2102 male offspring from 1093 litters. Of these, 907 females and 744 males survived for  $\geq 12$  months, enabling me to score them for dispersal or nondispersal (table S1). Of these 1651

survivors, 1315 (79.6%) showed natal philopatry and 336 (20.4%) showed natal dispersal (table S1). When dispersal occurred during the period when research assistants and I were at the study colony from March through June of every year, young prairie dogs always moved alone [ $N > 100$  dispersers; see also (17–21)].

For females of all three species, the probability of natal dispersal varied inversely and strongly with the number of close kin (mother, littermate sisters, and littermate brothers) within the natal territory (Fig. 1A). These striking inverse relationships resulted directly from the number of nearby close kin per se rather than from the number of nearby conspecifics, because a multiple logistic regression showed that the probability of natal dispersal did not vary significantly with clan size (the number of adults within the same territory, including not only close kin but also more distant kin and immigrants) for any species (for each species,  $t \leq 0.839$ ,  $P \geq 0.297$ ,  $N \geq 228$  dispersers and nondispersers). When compared to



**Fig. 1.** (A) Percentage of females that dispersed versus the number of close kin (mother, littermate sister, or littermate brother) in the natal territory. (B) Percentage of females that dispersed from the natal territory versus the presence or absence of close kin in that territory. (C) Percentage of males that dispersed versus the number of close kin in the natal territory. (D) Percentage of males that dispersed from the natal territory versus the presence or absence of close kin in that territory. For (A) and (C), values for  $t$  and  $P$  are from a multiple logistic regression that also considered the effect of clan size. For (B) and (D), values for  $\chi^2$  and  $P$  are from a  $2 \times 2$  chi-square test ( $df = 1$ ). All  $P$  values in the text and for Figs. 1 and 2 and fig. S1 are from two-tailed statistical tests. [Photos by Elaine Miller Bond]

females with  $\geq 1$  close kin within the natal territory, females with 0 nearby close kin were 12.5 times more likely to disperse for black-tailed prairie dogs, 5.5 times more likely for Gunnison's prairie dogs, and 2.5 times more likely for Utah prairie dogs (Fig. 1B).

Like young female prairie dogs, young males also were more likely to disperse when few or no close kin were present within the natal territory (Fig. 1, C and D). The effect of nearby close kin was weaker for males, however, and natal dispersal was significantly more common for males than for females for all three species (Fig. 2). Because of this sexual asymmetry in the frequency of dispersal and because both males and females were reluctant to copulate with close kin of the opposite sex living in the same territory (17–20), the frequency of incest with parents, offspring, or littermate siblings was  $<5\%$  for black-tailed and Gunnison's prairie dogs and  $<10\%$  for Utah prairie dogs (17–20). Figures 1 and 2 indicate that the reduced opportunity to cooperate with close kin and the importance of avoiding incest have both been important in the evolution of dispersal patterns of prairie dogs.

Determination of father-offspring kinships was more difficult than determination of mother-offspring and sibling-sibling kinships, because a female frequently copulated with more than one male during the period of 5 to 6 hours on the single day each year when she was sexually receptive (18, 20, 21). For the black-tailed prairie dog, the only species for which I had good behavioral and genetic information on paternity (18), natal dispersal by females was not significantly affected by the presence of the biological father in the natal territory ( $\chi^2 = 1.26$ ,  $P = 0.261$ ,  $N = 278$  dispersers and nondispersers).

The absence of close kin within the natal territory almost always encouraged dispersal by females, but the magnitude of the effect of each type of close kin varied (fig. S1). For example, female dispersal was significantly more likely in the absence of  $\geq 1$  littermate sister for all three species, and the disappearance of the mother significantly increased female dispersal for two of the three species. The absence of  $\geq 1$  littermate brother

tended to induce female dispersal for two species, but the effect was not significant for any species.

Clan territories were usually contiguous, and most prairie dogs ( $>50\%$  for both sexes for all three species) dispersed into an adjacent territory (17–21). Consequently, the typical costs of dispersal such as increased vulnerability to predation (2, 5, 9, 18) were probably lower for prairie dogs than for most other animals that usually disperse into more distant territories. This factor helps to explain why local dispersal in the absence of close kin within the natal territory was common and easy to document for the three species of prairie dogs (Figs. 1 and 2).

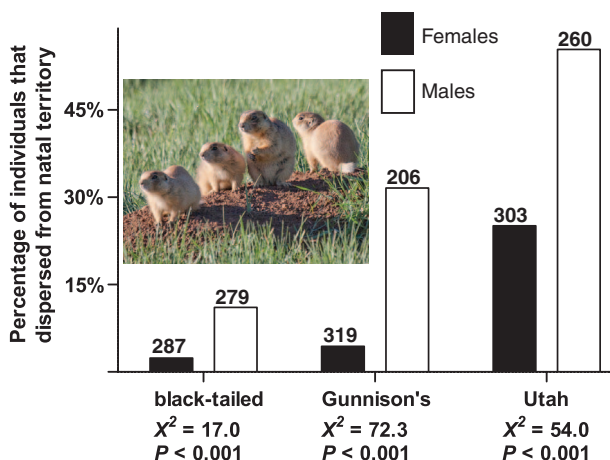
Some interactions among kin are competitive and costly, whereas others are cooperative and enhance survivorship and reproductive success (4, 8–13, 22, 23). For prairie dogs of all three species, competitive interactions with close kin of the same clan are frequent, and include fighting and chasing, ritualized disputes at territorial boundaries, and aggressive behaviors to commit or defend against infanticide (17–20, 24). Counteracting these competitive interactions are frequent cooperative behaviors among close kin, including the excavation and maintenance of elaborate burrow systems for rearing offspring and protection from predators and inclement weather; alarm calling when a large predator such as a coyote (*Canis latrans*) attacks; working together to chase a small predator such as a long-tailed weasel (*Mustela frenata*); and shared defense of the home territory against trespassing prairie dogs from adjacent territories (17–20). Another important cooperative behavior is communal nursing (the suckling of non-offspring), which can be life-saving for the unweaned offspring of close kin when the mother of those offspring dies from predation or some other cause (18, 25).

When the benefits of cooperation with kin within the natal territory exceed the costs of competition with those kin, the presence of close kin should promote natal philopatry, and the absence of close kin should promote natal dispersal. Natal philopatry of one or both sexes is common across many taxa (1–8, 22, 23, 26–29), but only one other study under natural conditions has shown

that natal dispersal is significantly more common when cooperating close kin are absent from the natal territory. Female yellow-bellied marmots (*Marmota flaviventris*,  $N = 231$  dispersers and nondispersers) were about 1.5 times more likely to disperse from the natal territory when the mother had disappeared [(30); see also (7) for supporting results from 23 laboratory-born desert night lizards, *Xantusia vigilis*, released into the wild].

When a young prairie dog's mother and littermate siblings all disappear because of death or dispersal, then the opportunity to benefit from cooperation with close kin within the natal territory also disappears; perhaps the absence of nearby close kin indicates that the natal territory is seriously inferior for some reason (such as recurring predation). In response to the absence of close kin within the natal territory, the results from this study show that young prairie dogs of three species are more likely to disperse in search of a new territory. When available, the best choice for a new territory might be one with the mother or a littermate sibling that has dispersed there previously, so that cooperation with close kin is again possible; 1 female black-tailed prairie dog, 3 female Gunnison's prairie dogs, and 10 female Utah prairie dogs made this choice. This option usually is not available, however, so the best alternative for most dispersers is probably a territory with more resources per individual, a lower probability of predation, or fewer intrusions by prairie dogs from adjacent territories. The absence of close kin in the natal territory is thus a proximate cause of natal dispersal by prairie dogs, but the ultimate cause is presumably the opportunity to find either a new territory that offers the benefits of cooperation with close kin that dispersed there previously (rare), or a new territory in which survivorship and reproductive success might be less dependent on cooperation with close kin (common).

**Fig. 2.** Sexual asymmetry in natal dispersal for three species of prairie dogs. Values for  $\chi^2$  and  $P$  are from a  $2 \times 2$  chi-square test ( $df = 1$ ). [Photo by Elaine Miller Bond]



## References and Notes

- K. E. Holekamp, *Ecology* **56**, 365 (1986).
- N. C. Stenseth, W. Z. Lidicker, Eds., *Animal Dispersal: Small Mammals as a Model* (Springer, New York, 2012).
- F. S. Dobson, A. T. Smith, W. X. Gao, *Behav. Ecol.* **9**, 622 (1998).
- X. Lambin, J. Aars, S. B. Piertney, in *Dispersal*, J. Clobert, E. Danchin, A. A. Shondt, J. D. Nichols, Eds. (Oxford Univ. Press, New York, 2001), pp. 110–122.
- D. E. Bowler, T. G. Benton, *Biol. Rev. Camb. Philos. Soc.* **80**, 205 (2005).
- L. J. Lawson Handley, N. Perrin, *Mol. Ecol.* **16**, 1559 (2007).
- A. R. Davis, *Behav. Ecol.* **23**, 18 (2012).
- T. H. Clutton-Brock, D. Lukas, *Mol. Ecol.* **21**, 472 (2012).
- W. D. Hamilton, R. M. May, *Nature* **269**, 578 (1977).
- W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
- R. Axelrod, W. D. Hamilton, *Science* **211**, 1390 (1981).
- S. A. West, I. Pen, A. S. Griffin, *Science* **296**, 72 (2002).
- T. G. Platt, J. D. Bever, *Trends Ecol. Evol.* **24**, 370 (2009).
- J. J. Jacquot, S. H. Vessey, *Behav. Ecol. Sociobiol.* **37**, 407 (1995).
- J. C. Moore, A. Loggenberg, J. M. Greeff, *Biol. Lett.* **2**, 17 (2006).
- J. Cote, J. Clobert, P. S. Fitze, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 9703 (2007).

17. J. L. Hoogland, *Science* **215**, 1639 (1982).
18. J. L. Hoogland, *The Black-tailed Prairie Dog: Social Life of a Burrowing Mammal* (Univ. of Chicago Press, Chicago, 1995).
19. J. L. Hoogland, *J. Mammal.* **80**, 243 (1999).
20. J. L. Hoogland, in *Rodent Societies*, J. O. Wolff, P. W. Sherman, Eds. (Univ. of Chicago Press, Chicago, 2007), pp. 438–450.
21. Details about my materials and methods are available as supplementary materials on Science Online.
22. J. B. Silk, *Philos. Trans. R. Soc. London Ser. B* **362**, 539 (2007).
23. J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, J. B. Silk, *The Evolution of Primate Societies* (Univ. of Chicago Press, Chicago, 2012).
24. J. L. Hoogland, *Behaviour* **69**, 1 (1979).
25. J. L. Hoogland, *Behav. Ecol. Sociobiol.* **63**, 1621 (2009).
26. P. J. Greenwood, *Anim. Behav.* **28**, 1140 (1980).
27. P. M. Waser, W. T. Jones, *Q. Rev. Biol.* **58**, 355 (1983).
28. W. D. Koenig, D. Van Vuren, P. N. Hooge, *Trends Ecol. Evol.* **11**, 514 (1996).
29. C. M. Arnaud, F. S. Dobson, J. O. Murie, *Mol. Ecol.* **21**, 493 (2012).
30. K. B. Armitage, D. H. Van Vuren, A. Ozgul, M. K. Oli, *Ecology* **92**, 218 (2011).

**Acknowledgments:** I thank J. Hoogland for encouraging me to reexamine my information on dispersal; my 150+ research assistants over the 31 years of research (especially my four offspring); and D. Boesch, K. Fuller, R. Gardner, R. Morgan, and L. Pitelka of the University of the Maryland Center for Environmental Science (UMCES) for the opportunity for long-term comparative research. Financial support was provided by Colorado Parks and Wildlife, the Denver Zoological Foundation, Environmental Defense, the Eppley Foundation, the Harry Frank Guggenheim Foundation, the National Fish and Wildlife Foundation, the National Geographic Society,

NSF, Princeton University, the Ted Turner Foundation, UMCES, and the Universities of Michigan and Minnesota. For help with the manuscript, I thank R. Alexander, D. Blumstein, D. Bowler, C. Brown, J. Clobert, T. H. Clutton-Brock, A. Davis-Robosky, F. S. Dobson, L. Handley, K. Holekamp, A. Hoogland, S. Keller, X. Lambin, M. Oli, P. Sherman, N. Solomon, and D. Van Vuren. Data for this report are archived as supplementary materials on Science Online.

#### Supplementary Materials

www.sciencemag.org/cgi/content/full/339/6124/1205/DC1  
Materials and Methods  
Fig. S1  
Tables S1 and S2  
References (31–38)

18 October 2012; accepted 23 January 2013  
10.1126/science.1231689

# Gene Transfer from Bacteria and Archaea Facilitated Evolution of an Extremophilic Eukaryote

Gerald Schönknecht,<sup>1,2\*</sup> Wei-Hua Chen,<sup>3,4†</sup> Chad M. Ternes,<sup>1†</sup> Guillaume G. Barbier,<sup>5†‡</sup> Roshan P. Shrestha,<sup>5†§</sup> Mario Stanke,<sup>6</sup> Andrea Bräutigam,<sup>2</sup> Brett J. Baker,<sup>7</sup> Jillian F. Banfield,<sup>8</sup> R. Michael Garavito,<sup>9</sup> Kevin Carr,<sup>10</sup> Curtis Wilkerson,<sup>5,10</sup> Stefan A. Rensing,<sup>11||</sup> David Gagneul,<sup>12</sup> Nicholas E. Dickenson,<sup>13</sup> Christine Oesterheld,<sup>14</sup> Martin J. Lercher,<sup>3,15</sup> Andreas P. M. Weber<sup>2,5,15\*</sup>

Some microbial eukaryotes, such as the extremophilic red alga *Galdieria sulphuraria*, live in hot, toxic metal-rich, acidic environments. To elucidate the underlying molecular mechanisms of adaptation, we sequenced the 13.7-megabase genome of *G. sulphuraria*. This alga shows an enormous metabolic flexibility, growing either photoautotrophically or heterotrophically on more than 50 carbon sources. Environmental adaptation seems to have been facilitated by horizontal gene transfer from various bacteria and archaea, often followed by gene family expansion. At least 5% of protein-coding genes of *G. sulphuraria* were probably acquired horizontally. These proteins are involved in ecologically important processes ranging from heavy-metal detoxification to glycerol uptake and metabolism. Thus, our findings show that a pan-domain gene pool has facilitated environmental adaptation in this unicellular eukaryote.

**A**lthough bacteria and archaea usually dominate extreme environments, hot and extremely acidic habitats are typically devoid of photosynthetic bacteria. Instead, eukaryotic unicellular red algae of the Cyanidiophyceae are the principal photosynthetic organisms in these ecological niches (1). Cyanidiophyceae can grow at pH 0 to 4 and temperatures up to 56°C, close to the upper temperature limit for eukaryotic life (2). *Galdieria sulphuraria* is a unique member of the Cyanidiophyceae, displaying high salt and metal tolerance and exhibiting extensive metabolic versatility (3, 4). *G. sulphuraria* naturally inhabits volcanic hot sulfur springs, solfatara soils, and anthropogenic hostile environments. In habitats with high concentrations of arsenic, aluminum, cadmium, mercury, and other toxic metals, *G. sulphuraria* frequently represents up to 90% of total biomass and almost all the eukaryotic biomass (1, 5).

To understand the molecular mechanisms underlying *G. sulphuraria*'s extremophilic and metabolically flexible lifestyle (Fig. 1), we determined its genome sequence (13.7 Mb; table S1)

(6). The only member of the Cyanidiophyceae for which a genome sequence was previously available, *Cyanidioschyzon merolae* (7), diverged from *G. sulphuraria* about 1 billion years ago, which approximates the evolutionary distance between fruit flies and humans (see fig. S1 and supplementary materials). *C. merolae* maintains a strictly photoautotrophic lifestyle and does not tolerate high salt or metal concentrations; it differs markedly from *G. sulphuraria* in ecology, cell biology, and physiology. Accordingly, we find orthologs for only 42% of the 6623 *G. sulphuraria* proteins in *C. merolae*, and only 25% of both genomes constitute syntenic blocks (fig. S2). Coding sequences make up 77.5% of the *G. sulphuraria* genome, resulting in a median intergenic distance of 20 base pairs (bp) (fig. S3). Protein-coding genes contain on average two introns (fig. S4), with median lengths of 55 bp (fig. S5). Thus, the *G. sulphuraria* genome is highly condensed by comparison with that of *C. merolae* and most other eukaryotes.

Eukaryotic innovations usually arise through gene duplications and neofunctionalizations, which

lead to expansion of existing gene families (8). In contrast, archaea and bacteria commonly adapt through horizontal gene transfer (HGT) from other lineages (9). HGT has also been observed in some unicellular eukaryotes (10); however, to our knowledge, horizontally acquired genes have not been linked to fitness-relevant traits in free-living eukaryotes (11). Phylogenetic analyses of *G. sulphuraria* genes using highly stringent criteria indicate at least 75 separate gene acquisitions from archaea and bacteria (supplementary materials). The origin of these *G. sulphuraria* genes from HGT is supported by the finding that compared to the genomic average, they have

<sup>1</sup>Department of Botany, Oklahoma State University, Stillwater, OK 74078, USA. <sup>2</sup>Institute of Plant Biochemistry, Heinrich-Heine-Universität Düsseldorf, 40225 Düsseldorf, Germany. <sup>3</sup>Institute for Computer Science, Heinrich-Heine-Universität Düsseldorf, 40225 Düsseldorf, Germany. <sup>4</sup>European Molecular Biology Laboratory (EMBL) Heidelberg, EMBL, Meyerhofstrasse 1, 69117 Heidelberg, Germany. <sup>5</sup>Department of Plant Biology, 612 Wilson Road, Michigan State University, East Lansing, MI 48824, USA. <sup>6</sup>Institut für Mathematik und Informatik, Ernst Moritz Arndt Universität Greifswald, Walther-Rathenau-Straße 47, 17487 Greifswald, Germany. <sup>7</sup>Department of Earth and Environmental Sciences, 4011 CC Little Building, 1100 North University Avenue, University of Michigan, Ann Arbor, MI 48109, USA. <sup>8</sup>Department of Earth and Planetary Science, Department of Environmental Science, Policy, and Management, University of California, Berkeley CA 94720–4767, USA. <sup>9</sup>Department of Biochemistry and Molecular Biology, 603 Wilson Road, Michigan State University, East Lansing, MI 48824, USA. <sup>10</sup>Research Technology Support Facility, Plant Biology Laboratories, 612 Wilson Road, Michigan State University, East Lansing, MI 48824, USA. <sup>11</sup>Faculty of Biology and BIOS Centre for Biological Signalling Studies, University of Freiburg, Schänzlestrasse 1, 79104 Freiburg, Germany. <sup>12</sup>UMR USTL-INRA 1281 "Stress Abiotiques et Différenciation des Végétaux cultivés," Université de Lille 1, 59650 Villeneuve d'Ascq Cédex, France. <sup>13</sup>Department of Microbiology and Molecular Genetics, Oklahoma State University, Stillwater, OK 74078, USA. <sup>14</sup>CyanoBiofuels GmbH, Magnusstrasse 11, 12489 Berlin, Germany. <sup>15</sup>Cluster of Excellence on Plant Sciences (CEPLAS), Heinrich-Heine-Universität Düsseldorf, 40225 Düsseldorf, Germany.

\*To whom correspondence should be addressed. E-mail: gerald.schoenknecht@okstate.edu (G.S.); andreas.weber@uni-duesseldorf.de (A.P.M.W.)

†These authors contributed equally to this work.

‡Permanent address: Novozymes, Inc, 1445 Drew Avenue, Davis, CA 95618, USA.

§Permanent address: Scripps Institution of Oceanography, University of California, San Diego, CA 92037, USA.

||Permanent address: Faculty of Biology, Philipps-Universität Marburg, 35032 Marburg, Germany.