

1 Human Impacts on Dissemination of Microbial Cells and Genes in the Biosphere

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27 For several billion years, microorganisms and the genes they carry have primarily been
28 moved by physical forces such as air and water currents. Three general drivers have
29 influenced their spread: opportunity for dispersal; stochasticity (numbers of foreign cells
30 arriving at a location); and recruitment (persistence of cells at the new location, often driven
31 by local selection). These forces have historically generated biogeographic patterns for
32 microorganisms that are similar to those of animals and plants (1). Humans have significantly
33 changed these dynamics. We perturb microbial populations by transporting large numbers of
34 cells to new locations, and by modifying selection pressures at those locations. As a
35 consequence, we are substantially altering microbial biogeography.

36 To give a sense of the scale of these effects, we can use one example, the class 1
37 integron. This DNA element acquires foreign genes from the environment, and has played a
38 central role in spreading antibiotic resistance between bacterial pathogens. DNA sequencing
39 data show that it had a single origin, in a single cell, sometime in the early 20th Century (2).
40 Derivatives of this original element can now be found in diverse bacterial species, resident in
41 many different vertebrate hosts, and on every continent. Millions to billions of copies of this
42 element now occur in every gram of feces from humans and domestic animals (Figure 1).
43 This spectacular increase in abundance and distribution has been driven by antibiotic
44 selection, increases in population, and dissemination via global transport. The numbers of
45 class 1 integrons released in waste streams mean that this DNA element has become a
46 significant pollutant across wide geographic areas, with up to 10^{23} copies being shed into the
47 environment every day (Figure 1) (3, 4).

48 The increasing abundance and distribution of the class 1 integron is just one example of the
49 genes and bacterial hosts now being disseminated by human activity. Key drivers for
50 increased dissemination of microorganisms include waste disposal, global transport and
51 tourism. Disposal of sewage increases the dissemination of both microorganisms and genes
52 (Figure 1) (5). Some 35.9 Mha of croplands are dependent on irrigation with urban
53 wastewater, 80% of which undergoes little, or no treatment (6). Use of wastewater or manure
54 in agriculture contaminates fruits, vegetables and farm animals, that are then distributed
55 globally via the food-supply chain (7).

56 Wastewater carries high densities of microorganisms and their cargo genes. It also contains
57 significant concentrations of compounds with biological effects, including metals, antibiotics
58 and disinfectants (8). The simultaneous dispersal of microorganisms and selective agents
59 increases mutation rates in these microbial populations, enhancing their evolvability. This
60 allows them to respond dynamically to changing environments by generating *de novo*
61 variability, which in turn is likely to confer adaptive advantages on at least a subset of cells
62 arriving at a new location. Co-selection on different cargo genes amplifies this effect. For
63 example, diverse genes for resistance to metals and disinfectants are often closely linked to
64 multiple antibiotic-resistance genes on the same genetic element. Exposure to selective agents
65 maintains these clusters of resistance determinants (5), greatly increasing the probability of
66 selection at a destination, and improving the chances of recruitment after dispersal.

67 Humans and animals now move on an unprecedented scale, and this movement actively
68 transports and enriches a specific subset of microorganisms. Humans and agricultural animals
69 now comprise 35-fold more biomass than wild terrestrial mammals (9), so the bacteria shed
70 in feces mainly represent the gut microbiota of humans, cattle, sheep, goats, pigs, and
71 chickens. These specific gut microorganisms have vastly increased in both abundance and
72 distribution, particularly in the last century. Efficiency of dispersal is enhanced by the 1.2
73 billion international tourist movements per year, evidenced by the rapid spread of bacterial
74 clones and genes conferring antibiotic resistance between continents (10).

75 Humans also promote dispersal of microbial cells via mass movement of materials. Ballast
76 water from commercial shipping moves diverse microorganisms around the globe. An
77 estimated 100 million tonnes of ballast water is discharged each year into US ports alone,
78 giving some indication of the volumes involved (11). Human activities now move more soil,
79 sand and rock than all natural processes combined. Natural fluvial erosion is 21 Gt/y, much
80 lower than the 75 Gt/y eroded by agriculture (12). This erosion transports vast numbers of
81 microorganisms, especially in soil.

82 Understanding how human activities cause systematic changes in ecosystems is increasingly
83 important, particularly in regard to our effects on biogeochemistry driven by microorganisms
84 (13). Such studies involve a concerted effort to link the distribution and composition of
85 biodiversity with biogeochemical processes at landscape scales and with belowground
86 ecosystem functions (14).

87 Linking the rapidly expanding databases generated by environmental genomics with the
88 construction of biogeochemical models is increasingly important. Fusion of genomics and
89 Earth system science is a first step to understanding how the biochemical functions of
90 microorganisms could be altered, temporally and spatially, by global change (15). In
91 particular, fixation of atmospheric nitrogen into biologically available forms, and global
92 carbon dioxide and methane emissions are strongly affected by human activity. The dynamics
93 of the microbial nitrogen cycle will be perturbed by industrial nitrogen fixation, while
94 warming of wetlands and thawing of permafrost will release large quantities of microbially
95 generated methane.

96 There are complex feedbacks between microbial activities, dispersal of cells and genes,
97 natural selection, and the interactions between physical, chemical, geological and human
98 processes. Understanding these is a grand challenge for this century. Progress can only be
99 made by forming new, interdisciplinary research teams that can manage and interpret the
100 enormous data sets required. These data sets can then be applied to the complex, multi-gene
101 phenotypes that are centrally important to global biogeochemistry and human health.

102 There is a growing, and recent trend for monitoring the environmental dissemination of
103 genes, particularly those that confer phenotypes of direct relevance to human and animal
104 health. Much of this work has focused on the clusters of resistance genes that have been
105 assembled under the aegis of human selection pressure (5). Realization of the global extent of
106 pollution with these xenogenetic elements (3), and the organisms that carry them, should now
107 stimulate much more global questions. Investigations into microbial invasions, microbial
108 extinctions, and perturbations to microbial ecosystems are now a high priority. In particular,
109 monitoring and improvements in waste water and manure treatments are critical.

110 Microorganisms usually perform their essential ecosystem services invisibly, but we ignore
111 them at our peril.

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113 **References**

- 114 1. S. Evans, J. B. Martiny, S. D. Allison, Effects of dispersal and selection on stochastic assembly
115 in microbial communities. *The ISME Journal* **11**, 176-185 (2017).
- 116 2. M. R. Gillings *et al.*, Using the class 1 integron-integrase gene as a proxy for anthropogenic
117 pollution. *The ISME Journal* **9**, 1269-1279 (2015).
- 118 3. Y.-G. Zhu *et al.*, Continental-scale pollution of estuaries with antibiotic resistance genes.
119 *Nature Microbiology* **2**, 16270 (2017).

- 120 4. M. R. Gillings, Class 1 integrons as invasive species. *Current Opinion in Microbiology* **38**, 10-
121 15 (2017).
- 122 5. T. A. Johnson *et al.*, Clusters of Antibiotic Resistance Genes Enriched Together Stay Together
123 in Swine Agriculture. *mBio* **7**, e02214-02215 (2016).
- 124 6. A. L. Thebo, P. Drechsel, E. Lambin, K. Nelson, A global, spatially-explicit assessment of
125 irrigated croplands influenced by urban wastewater flows. *Environmental Research Letters*
126 **12**, 074008 (2017).
- 127 7. J. Bengtsson-Palme, Antibiotic resistance in the food supply chain: Where can sequencing
128 and metagenomics aid risk assessment? *Current Opinion in Food Science* **14**, 66-71 (2017).
- 129 8. Z. Tousova *et al.*, European demonstration program on the effect-based and chemical
130 identification and monitoring of organic pollutants in European surface waters. *Science of*
131 *the Total Environment* **601**, 1849-1868 (2017).
- 132 9. V. Smil, Harvesting the biosphere: The human impact. *Population and Development Review*
133 **37**, 613-636 (2011).
- 134 10. J. Bengtsson-Palme *et al.*, The human gut microbiome as a transporter of antibiotic
135 resistance genes between continents. *Antimicrobial Agents and Chemotherapy* **59**, 6551-
136 6560 (2015).
- 137 11. D. S. Lympelopoulou, F. C. Dobbs, Bacterial Diversity in Ships' Ballast Water, Ballast-Water
138 Exchange, and Implications for Ship-Mediated Dispersal of Microorganisms. *Environmental*
139 *Science & Technology* **51**, 1962-1972 (2017).
- 140 12. B. H. Wilkinson, B. J. McElroy, The impact of humans on continental erosion and
141 sedimentation. *Geological Society of America Bulletin* **119**, 140-156 (2007).
- 142 13. Y.-G. Zhu, B. J. Reid, A. A. Meharg, S. A. Banwart, B.-J. Fu, Optimizing Peri-URban Ecosystems
143 (PURE) to re-couple urban-rural symbiosis. *Science of The Total Environment* **586**, 1085-1090
144 (2017).
- 145 14. K. Küsel *et al.*, How deep can surface signals be traced in the critical zone? Merging
146 biodiversity with biogeochemistry research in a central German Muschelkalk landscape.
147 *Frontiers in Earth Science* **4**, 32 (2016).
- 148 15. T. Mock *et al.*, Bridging the gap between omics and earth system science to better
149 understand how environmental change impacts marine microbes. *Global Change Biology* **22**,
150 61-75 (2016).

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