

# Bioprecipitation: a feedback cycle linking earth history, ecosystem dynamics and land use through biological ice nucleators in the atmosphere.

Cindy E. Morris, Franz Conen, J. Alex Huffman, Vaughan T. J. Phillips,  
Ulrich Poschl, David Sands

► **To cite this version:**

Cindy E. Morris, Franz Conen, J. Alex Huffman, Vaughan T. J. Phillips, Ulrich Poschl, et al.. Bioprecipitation: a feedback cycle linking earth history, ecosystem dynamics and land use through biological ice nucleators in the atmosphere.. Global Change Biology, Wiley, 2014, 20 (2), pp.341-351. 10.1111/gcb.12447 . hal-02637995

**HAL Id: hal-02637995**

**<https://hal.inrae.fr/hal-02637995>**

Submitted on 28 May 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



1 Running head: Bioprecipitation feedback cycle

---

2  
3 **Bioprecipitation: A feedback cycle linking Earth history, ecosystem dynamics**  
4 **and land use through biological ice nucleators in the atmosphere**  
5

6 Cindy E. Morris<sup>1,2\*</sup>, Franz Conen<sup>3</sup>, J. Alex Huffman<sup>4</sup>, Vaughan Phillips<sup>5</sup>, Ulrich Pöschl<sup>6</sup>,  
7 David C. Sands<sup>2</sup>

8 <sup>1</sup>INRA, UR0407 Pathologie Végétale, F-84143 Montfavet cedex, France

9 <sup>2</sup>Dept. Plant Sciences and Plant Pathology, 119 Plant Bioscience Bldg., Montana State  
10 University, Bozeman, MT 59717-3150, USA

11 <sup>3</sup>Department of Environmental Sciences, University of Basel, 4056 Basel, Switzerland

12 <sup>4</sup>University of Denver, Department of Chemistry and Biochemistry, Denver, CO, 80208, USA

13 <sup>5</sup>Department of Physical Geography and Ecosystem Science, Lund University, Solvegatan 12,  
14 223 62 Lund, Sweden

15 <sup>6</sup>Max Planck Institute for Chemistry, Biogeochemistry and Multiphase Chemistry Departments,  
16 55128 Mainz, Germany

17

18 **\*Corresponding author:**

19 tel: +33 (0)4 32 72 28 41, fax: +33 (0)4 32 72 28 42 [cindy.morris@avignon.inra.fr](mailto:cindy.morris@avignon.inra.fr)

20 **Keywords:** biological ice nucleation, cloud physics, ice multiplication, aerobiology,

21 *Pseudomonas syringae*, rainfall

22 **Type of paper:** Opinion

23

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

### 24 **Abstract:**

25 Landscapes influence precipitation via the water vapor and energy fluxes they generate.

26 Biologically active landscapes also generate aerosols containing microorganisms, some being

27 capable of catalyzing ice formation and crystal growth in clouds at temperatures near 0° C. The

28 resulting precipitation is beneficial for the growth of plants and microorganisms. Mounting

29 evidence from observations and numerical simulations support the plausibility of a

30 bioprecipitation feedback cycle involving vegetated landscapes and the microorganisms they

31 host. Furthermore, the evolutionary history of ice nucleation active bacteria such as

32 *Pseudomonas syringae* supports that they have been part of this process on geological time scales

33 since the emergence of land plants. Elucidation of bioprecipitation feedbacks involving

34 landscapes and their microflora could contribute to appraising the impact that modified

35 landscapes have on regional weather and biodiversity, and to avoiding inadvertent, negative

36 consequences of landscape management.

37

38

39

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

40 Microorganisms have long played important roles in the Earth system. For example, the most  
41 important change in the history of Earth's climate, and the most significant for life on our planet,  
42 was the rise in atmospheric O<sub>2</sub> concentration from 2% about 2.3 billion years ago (Gya) to the  
43 current concentration of 20% (Kasting & Siefert, 2002), caused primarily by microorganisms.  
44 They are also currently responsible for about 70% of the greenhouse gas methane released into  
45 the atmosphere (Conrad, 2009), and for production of nitrogen oxides and of the precursor of  
46 dimethylsulfide, a major source of atmospheric sulfur (Bates *et al.*, 1992). In light of these and  
47 other roles in Earth system process, the American Academy of Microbiology recently and  
48 justifiably pointed out the need to integrate microbiology more closely with the study of climate  
49 processes (Reid, 2011). Their report called for enhanced interdisciplinary collaboration on a  
50 range of biogeochemical processes, yet it neglected processes whereby microorganisms influence  
51 climate (cloud and rainfall patterns in particular) via their impact on atmospheric chemistry and  
52 physics.

53 Over the past decade interest has grown in the so-called bioprecipitation hypothesis: a feedback  
54 cycle whereby land plants generate small airborne particles (aerosols) containing plant-associated  
55 microorganisms that influence formation and evolution of clouds via their ice nucleation activity,  
56 leading to precipitation that in turn is beneficial for plant and microbial growth (Sands *et al.*,  
57 1982) (Figure 1.). The renewed interest in this hypothesis has been ignited, in part, by the  
58 surging need for more precise quantification of cloud evolution for models of global climate  
59 change and by recurring droughts and desertification. Part of this renewed effort has been to  
60 assemble the evidence that ice nucleation active (INA) microorganisms indeed affect the  
61 microphysical processes in clouds leading to rainfall (Szyrmer & Zawadzki, 1997; Möhler *et al.*,  
62 2007; DeMott & Prenni, 2010; Morris *et al.*, 2011; Murray *et al.*, 2012). The effect of

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

63 microorganisms on the microphysical processes in clouds is one essential component of  
64 bioprecipitation. But there has been little effort to illustrate how it is part of greater Earth system  
65 processes. In this paper we go beyond previous reviews of microbial ice nucleation by bringing  
66 together current information supporting that microbial-induced ice nucleation in clouds is directly  
67 linked to a feedback cycle with plants, and by illustrating how this cycle benefits from auxiliary  
68 processes that reinforce ice nucleation activity in microorganisms. As landscapes are modified  
69 by human activities, and as the ranges of habitats of plants change with the changing climate of  
70 the Earth, feedback cycles could lead to unexpected consequences. Elucidation of precipitation  
71 feedbacks involving landscapes and their microflora could contribute to appraising the impact  
72 that modified landscapes have on regional weather and biodiversity, and to avoiding inadvertent,  
73 negative consequences of landscape management. Therefore, we believe that concerted effort for  
74 such elucidation is needed.

### 75 **The essential components of a bioprecipitation cycle**

76 Knowledge of well-known environmental processes led Sands and colleagues (Sands *et al.*, 1982)  
77 to propose the bioprecipitation cycle over 30 years ago. Recently, there have been reports of  
78 additional phenomena associated with the two basic components of this feedback cycle that add  
79 credibility to its existence.

80  
81 Component 1: Plants emit water vapor and release microorganisms into the atmosphere. The  
82 water vapor emitted from plants is essential for cloud formation and ice nuclei are critical for  
83 rainfall. Among the microorganisms released are INA strains of various species of bacteria and  
84 fungi (Morris *et al.*, 2004; Murray *et al.*, 2012), and these microorganisms can be transported to  
85 the altitude of clouds as aerosols. A wide range of microorganisms has been observed directly in

86 cloud water, including bacteria and fungi known to be INA (Amato *et al.*, 2007; Joly *et al.*,  
87 2013). Laboratory studies have shown that the harsh conditions endured during ascent and  
88 residence in the atmosphere are not detrimental to bacterial ice nucleation activity (Attard *et al.*,  
89 2012). The potential efficiency of microbial ice nuclei in this role has been the subject of the  
90 numerous reviews indicated above.

91  
92 Component 2: Rainfall provides water for growth of plants and for multiplication of  
93 microorganisms. The latter benefit from increased plant mass and directly from the availability  
94 of water. Plant water vapor and microorganisms can then feed back into the first component of  
95 the cycle. The idea of the bioprecipitation cycle arose from the obvious beneficial impact of rain  
96 on plant growth and the subsequent enhanced growth of microorganisms due to the increased  
97 availability of plant tissue. Furthermore, it is well-known that wet conditions favor nearly all  
98 diseases of leaf tissue caused by fungi or bacteria (with the exception of the powdery mildews  
99 that proliferate in dry weather) including those caused by INA microorganisms that are also plant  
100 pathogens (bacteria and rust fungi, for example) (Agrios, 2005). More specifically, studies of  
101 molecular mechanisms of plant disease resistance have revealed, for the case of the INA  
102 bacterium *Pseudomonas syringae* in particular, that plants interfere with the growth of bacterial  
103 pathogens by restricting their access to water at the cellular level (Freeman & Beattie, 2009),  
104 further illustrating the critical role of water limitation in the multiplication of plant-associated  
105 bacteria. As a corollary to these phenomena, heavy rainfalls ( $\geq 20$  mm) result in thousand-fold  
106 increases in population sizes of *P. syringae* on leaves within 48 hours, and these increased  
107 densities can persist for weeks before declining (Hirano *et al.*, 1996). It is reasonable to assume  
108 that as population sizes of microorganisms on leaves increase, the emission of microorganisms

109 from these leaves increases. However, there has not been a formal demonstration of this  
110 phenomenon, mostly due to the paucity of studies of microbial flux in the atmosphere (Morris *et*  
111 *al.*, 2013a). Nevertheless, in one of the few studies of microbial flux, upward flux over crops was  
112 the highest over the crops having the most dense microbial populations on their leaves  
113 (Lindemann *et al.*, 1982). Overall, plant quality affects the abundance of biological ice nuclei in  
114 the atmosphere, with the greatest concentrations being observed over agricultural land than over  
115 suburban land or forests (Bowers *et al.*, 2011). Finally, rainfall is followed by enrichment of ice  
116 nuclei in the atmosphere (Bigg, 1958; Constantinidou *et al.*, 1990; Huffman *et al.*, 2013; Prenni  
117 *et al.*, 2013; Tobo *et al.*, 2013) some of which are microbial.

118 The framework for the bioprecipitation cycle has been largely inspired by knowledge of the  
119 emission of ice nucleation active microorganisms such as *P. syringae* and rust fungi from plants  
120 and their transport through the atmosphere and clouds. Nevertheless, this cycle is pertinent for  
121 any biological INA particle whose abundance increases as a feedback response to the  
122 precipitation that it initiated. Therefore, INA particles implicated in a bioprecipitation cycle  
123 would have to multiply by reproduction at least during some part of the cycle, although they  
124 could be functionally incapable of reproduction by the time in the cycle that emission or  
125 glaciation occurred. Many different types of biological ice nuclei have been detected in the  
126 atmosphere but, to date, only a few of them have been specifically linked to the full set of  
127 processes involved in the bioprecipitation cycle (Figure 1).

### 128 **The impact of biological ice nuclei on cold clouds – a contentious issue**

129 The real impact of INA microorganisms on cloud microphysics and subsequent precipitation has  
130 been a subject of contention. There is generally agreement that the atmospheric processes  
131 leading to interaction of ice nuclei and super cooled cloud droplets could set INA

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

132 microorganisms into the appropriate context to catalyze freezing, and this has been substantiated  
133 by direct observation of such microorganisms in clouds as indicated above. However, the crux of  
134 the debate is whether there are sufficient numbers of biological ice nuclei in clouds to set off a  
135 process that renders measurable precipitation.

136 There are two main pathways by which precipitation forms in natural clouds. The “warm rain  
137 process” involves collisions between cloud droplets of differing sizes and fall speeds, resulting in  
138 coalescence. The warm rain process tends to dominate precipitation production in deep  
139 convective clouds with warm bases and rapid ascent > 1 m/s aloft (Phillips *et al.*, 2001, 2005).

140 The “ice crystal process” involves nucleation of ice followed by vapor growth of crystals, riming  
141 of supercooled droplets and aggregation of ice. This type of precipitation is sensitive to active  
142 concentrations of ice nuclei (Phillips *et al.*, 2003). Horizontally extensive stratiform (non-  
143 convective) clouds that contain ice and are mixed-phase (liquid and ice co-existing), such as  
144 frontal nimbostratus clouds, can generate precipitation by this ice-crystal process. In the present-  
145 day climate, mixed-phase nimbostratus clouds (and thus the cold-rain process) are more common  
146 at mid- and high latitudes than in the tropics and sub-tropics (Rossow & Schiffer, 1999; Hahn *et*  
147 *al.*, 2001). Their slow ascent (< 1 m/s) and longevity (lifetimes of many hours) allow ice crystals  
148 to fall, to grow by vapor deposition and consequently to become precipitation in the form of ice  
149 that may melt.

150 When the cloud top is warmer than about -37° C, nimbostratus precipitation is predicted to be  
151 boosted by higher total concentrations of all active ice nuclei - biological, mineral or others  
152 (Phillips *et al.*, 2003). It is under such conditions that INA microorganisms could be involved in  
153 the freezing process and hence in precipitation. A role for INA microorganisms is especially  
154 expected for glaciated clouds with tops too warm for INA dust to be prolific (warmer than about



## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-351. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

155 -15 to -20 °C). For clouds with colder tops, the few estimates available suggest that the  
156 abundance of active bacterial ice nuclei (those active at warmer than ca. -10° C) in the remote  
157 free troposphere over continental regions (Bowers *et al.*, 2009) is typically at least two orders of  
158 magnitude lower than that of mineral or other non-biological ice nuclei active at much colder  
159 temperatures (colder than -20° C) (DeMott *et al.*, 2003) and might be insufficient to influence  
160 precipitation. However, INA microorganisms can benefit from a process of ice multiplication  
161 that is restricted to a very specific temperature range, if their primary ice can grow to become ice  
162 precipitation aloft. Between -3° and -8° C, the number of ice particles in clouds can be amplified  
163 by the Hallett-Mossop (H-M) process of ice multiplication (Hallett & Mossop, 1974; Harris-  
164 Hobbs & Cooper, 1987), which involves rime-splintering of ice precipitation leading to ice  
165 concentrations that are several orders of magnitude greater than what would be expected due to  
166 primary ice nucleation alone (Bower *et al.*, 1996). Indeed, such impacts from biological ice  
167 nuclei on the H-M process have been simulated (Phillips *et al.*, 2009). Virtually none of the non-  
168 biological ice nuclei naturally present in the atmosphere, such as mineral dust (active when colder  
169 than -10 to -20° C) (Ansmann *et al.*, 2008; DeMott *et al.*, 2011) or soot (active when colder than  
170 -20° C) (DeMott, 1990), can prolifically catalyze ice formation in the temperature range of the H-  
171 M process (Hallett & Mossop, 1974), whereas INA bacteria clearly catalyze ice formation in this  
172 temperature range and under conditions simulating clouds (Möhler *et al.*, 2008).

173 One of the first global modeling studies of biological ice nuclei predicted that their contribution  
174 to the global average ice nucleation rate is very small ( $10^{-5}$ - 0.6%) (Hoose *et al.*, 2010).  
175 However, this study doesn't take ice multiplication effects such as the H-M effect or rime  
176 splintering into account, and there is much uncertainty about how to simulate biological ice  
177 nuclei. This global study was based on properties of a specific strain of *P. syringae* recently

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-351. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

178 shown to have IN efficiencies much lower (by at least about 3 orders of magnitude) than many  
179 other strains of this bacterium (Murray *et al.*, 2012). Moreover, a separate empirical  
180 parameterization of ice nucleation by aerosol species predicts that 3-6% of all active ice nuclei at  
181  $-30^{\circ}\text{C}$  are biological in the continental background troposphere based on observations of very  
182 large samples of many strains of naturally-occurring *P. syringae* (Phillips *et al.*, 2008, 2013).  
183 This parameterization was validated against coincident field measurements of active biological  
184 ice nuclei and bio-aerosol particles in Colorado (Phillips *et al.*, 2013). At least over certain  
185 continental regions such as the tropical rainforest basin in the Amazon, the formation of ice and  
186 precipitation in deep stratiform clouds and convective clouds with cold bases and tops warmer  
187 than about  $-15$  to  $-20^{\circ}\text{C}$  (ice nuclei from dust have little activity at temperatures warmer than  
188 this), and the glaciation of deep convective clouds with warm bases, are all likely triggered by  
189 biological particles. In such clouds, biological ice nuclei are present and in some cases may  
190 prevail in the overall initiation of primary ice ( Prenni *et al.*, 2009; Pöschl *et al.*, 2010).  
191 The growing pool of data on abundance of microbial ice nuclei in the atmosphere portends the  
192 emergence of more studies illustrating regional impacts of these ice nuclei on precipitation.  
193 (Phillips *et al.*, 2013; Prenni *et al.*, 2013). However, there will be further points of contention to  
194 resolve. First, not all particles carrying surfaces of biological origin and capable of catalyzing ice  
195 formation at warm temperatures ( $> -10^{\circ}\text{C}$ ) are microorganisms launched from plant surfaces.  
196 Another form of biological IN includes decomposed organisms, or parts thereof, attached to soil  
197 minerals (Conen *et al.*, 2011; O'Sullivan *et al.*, 2013). Soil organic matter typically has a turnover  
198 time of decades to centuries. Abundance and IN activity associated with it are unlikely affected  
199 by precipitation events in the short term and therefore unlikely to play a role in bioprecipitation  
200 as we understand it. Second, the presence of INA microorganisms in clouds is proof that they are

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

201 transported up to the altitude of clouds (Amato *et al.*, 2007; Joly *et al.*, 2013). But there are few  
202 data available about how this happens – about the conditions that are favorable for this transport  
203 and about real measured rates of transport from different sources. Furthermore, some of the  
204 available data seem to contradict each other. In the only reported direct measurement of flux of  
205 INA microorganisms into the atmosphere, they ascended at  $72 \text{ cells m}^{-2} \text{ min}^{-1}$ . The bacterium *P.*  
206 *syringae* contributed 75% of this INA aerosol (Lindemann *et al.*, 1982). Under these same  
207 conditions, INA *P. syringae* was found in aerosols at canopy height at concentrations of about 6  
208  $\text{cells m}^{-3}$  in a snap bean field having on average  $2.7 \times 10^6$  INA *P. syringae* per gram of leaf. This  
209 microbial aerosol concentration is at the limit of sensitivity of sampling and detection methods  
210 available in aerobiology and illustrates why there have been such few reports of successful  
211 detection of *P. syringae* or other INA microorganisms in dry aerosols. Under conditions where  
212 INA *Pseudomonas* spp. were present on plant canopies, Garcia and colleagues failed to detect  
213 these bacteria in most samples of aerosols collected downwind of the suspected source fields and  
214 were successful only during combine harvesting of the fields (Garcia *et al.*, 2012). Although the  
215 authors were surprised by this result, it can be explained by the differences in detection  
216 thresholds of the technique they used compared to that of Lindemann and colleagues. Garcia and  
217 colleagues used a direct molecular detection method based on polymerase chain reaction (PCR)  
218 amplification of the gene for ice nucleation activity (the *ina* or the *ice* gene) in *Pseudomonas* spp.  
219 The detection threshold of this technique, according to the reported methods, was 0.1 copies of  
220 the targeted gene per liter of air. It can be assumed that cells of *Pseudomonas* spp. carry 1 copy  
221 of the *ina* or *ice* gene per cell, therefore this threshold is equivalent to  $0.1 \text{ cells L}^{-1}$ . In contrast,  
222 using microbiological culture media, Lindemann and colleagues could detect as few as  $0.001$   
223 bacterial cells  $\text{L}^{-1}$ . When Garcia and colleagues detected INA bacteria in air samples during  
224 combine harvesting of the agricultural fields at their experimental site, a context where high

225 quantities of aerosols are generated, the concentrations were about 19 cells L<sup>-1</sup>. This represented  
226 2 orders of magnitude above their own detection limit and 4 orders of magnitude more than the  
227 concentrations observed by Lindemann and colleagues during the crop growth season. Hence, it  
228 is likely that atmospheric concentrations of INA bacteria were below the limits of detection for  
229 most of the sampling times in the study of Garcia and colleagues thereby giving the impression  
230 that they were not present as aerosols. The sensitivity of detection methods for INA  
231 microorganisms in the atmosphere is not the only problem that will complicate the debate about  
232 the role of these microorganisms in precipitation. As described in previous work (Morris *et al.*,  
233 2012) thermal plumes can have an important role in the upward flux of microorganisms from  
234 plant surfaces. These plumes are “packages” of air that can uplift the associated aerosols without  
235 marked dilution and they are not uniformly distributed across a landscape. The results of such a  
236 phenomenon have in fact been observed in the dissemination of fungi (Hirst *et al.*, 1967). The  
237 resulting uneven and aggregated distribution of aerosols suggests that air samples might not  
238 necessarily reflect the spatial and temporal variability of atmospheric microbial concentrations.

239

240 **Favorable environmental contexts for the emergence and maintenance of a bioprecipitation**  
241 **cycle**

242 Atmospheric circulation of heat and water vapor and the distribution of clouds have changed over  
243 Earth’s history. The dramatic changes leading to modern atmospheric circulation began about  
244 100 million years ago with the break-up of Pangea during the Cretaceous period. Poleward shifts  
245 of land masses and the uprising of mountains contributed to ascent and adiabatic cooling of rising  
246 air over the newly created continents (DeConto, 2008) thereby leading to sub-zero temperatures  
247 in clouds at mid and high latitudes over these continents in contrast to the arid desert that had

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

248 covered much of the interior of Pangea previously. The changing climatic conditions were  
249 accompanied by an expansion across mid- and high latitudes of terrestrial angiosperms and, in  
250 particular, temperate forests (Zhou *et al.*, 2012). This set in place conditions that could have been  
251 exploited by plant-associated INA microorganisms. Data on the evolutionary history of the gene  
252 conferring ice nucleation activity in bacteria and of the major class of bacteria that possess this  
253 gene, the  $\gamma$ -Proteobacteria, suggest that as of the Cretaceous period of Earth's history all of the  
254 fundamental conditions were in place for INA  $\gamma$ -Proteobacteria to play a role in ice-induced  
255 rainfall.

256 Although the ability to catalyze the freezing of water above the temperature of spontaneous  
257 freezing (ca.  $-37^{\circ}\text{C}$ ) (Murray *et al.*, 2010) is a property of various organisms, non-living organic  
258 compounds and minerals (Mossop, 1963; Morris *et al.*, 2004; Murray *et al.*, 2012), the most is  
259 known about this capacity for the class of bacteria called the  $\gamma$ -Proteobacteria. Strains of these  
260 bacteria catalyze freezing at the warmest temperatures of all the INA materials regularly found in  
261 the environment (Murray *et al.*, 2012). An outer membrane protein orients water molecules into  
262 the cubic form of ice that spontaneously converts to hexagonal ice (Kajava, 1995) in a process  
263 that resembles the recently discovered shift from cubic to hexagonal ice that can occur during the  
264 spontaneous freezing of water in the atmosphere (Murray *et al.*, 2005). The most plausible origin  
265 of the gene for the INA protein in the  $\gamma$ -Proteobacteria is from a common ancestor of the highly  
266 divergent orders of bacteria in which it has been described: Xanthomonadales, Pseudomonadales,  
267 Enterobacteriales (Wolber, 1993). This allows us to estimate that the gene has been part of the  $\gamma$ -  
268 Proteobacteria since sometime between the emergence of this class of bacteria (ca. 1.75 Gya  
269 (Battistuzzi *et al.*, 2004)) and the diversification of some of the youngest genera in this class (0.5  
270 Gya (Lerat *et al.*, 2003)). During this part of Earth's history there were significant periods of

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

271 glaciation (Fig. 2). This provided millions of years of opportunity for the INA protein to interact  
272 with freezing water.

273 One of the most intriguing aspects of bacterial ice nucleation activity is its efficiency relative to  
274 that of mineral particles or of other biological ice nuclei. INA  $\gamma$ -Proteobacteria have orders of  
275 magnitude more ice active sites per surface area of their cells than fungi or birch pollen or when  
276 compared in terms of surface area to inert particulate matter such as ash, dust, soot and other INA  
277 minerals (Murray *et al.*, 2012). It is likely that the remarkable ice nucleation activity of these  
278 bacteria results from cycles of natural selection during the evolution of the  $\gamma$ -Proteobacteria. A  
279 hallmark of natural selection on a trait is that it causes the trait to be markedly less variable  
280 among strains within specific genetic lineages of a population than between different genetic  
281 lineages (Nielsen, 2005). Interestingly, INA is not a uniform trait across the  $\gamma$ -Proteobacteria  
282 class or even within the *P. syringae* species complex nor does it seem to be a randomly  
283 distributed capacity among the different strains of these groups. Certain genetic lineages of *P.*  
284 *syringae*, for example, clearly have higher frequencies of very efficient INA strains than other  
285 lineages (Morris *et al.*, 2010) corroborating the importance of positive natural selection in the  
286 evolution of this trait.

287 There are several ways in which catalysis of freezing could have been an advantage for the  
288 fitness of bacteria in the  $\gamma$ -Proteobacteria class. It should be noted that there is no evidence for  
289 other functions of the ice nucleation protein beyond being INA (Wolber, 1993) and thus the  
290 fitness advantages of freezing would have, in themselves, led to positive natural selection of ice  
291 nucleation activity. During their early evolution before the emergence of life on land, the  $\gamma$ -  
292 Proteobacteria were aquatic organisms. The advantage of INA in aquatic habitats has likely been  
293 due to the enhanced survival gained by managing ice formation outside of the cell wall.

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

294 Nucleation of ice outside of the cell, whether provoked by an organism itself or induced during  
295 procedures of cryoconservation, is an effective method of protecting cells during freezing events  
296 in the ambient environment (Fahy, 1995; Zachariassen & Kristiansen, 2000). In aquatic habitats,  
297 freezing might also be a means to increase access to nutrients. It has been shown that microbial  
298 INA is responsible for the formation of frazil ice in aggregates of diatoms and bacteria. This is  
299 thought to benefit the bacteria associated with the aggregates because the frazil ice floats to the  
300 surface where the diatoms have greater access to light thereby producing more photosynthates  
301 that are food for the associated bacteria (D'Souza *et al.*, 2013). Presently, aquatic milieus are still  
302 habitats for INA bacteria. INA *Pseudomonas* spp. have been found in salt water (Fall & Schnell,  
303 1985) and in a supraglacial stream in Antarctica (Foreman *et al.*, 2013), and INA *P. syringae* are  
304 abundant in fresh water (Morris *et al.*, 2008, 2010). When INA bacteria became associated with  
305 land plants, one likely impact of ice nucleation activity has been the gain in fitness from  
306 nutrients released from leaf tissue damaged during ice formation (Wolber, 1993).

307 It has been proposed that, by inducing precipitation, INA microorganisms also procure a gain in  
308 fitness that leads to positive selection of ice nucleation activity (Wolber, 1993; Morris *et al.*,  
309 2010, 2012). This idea is supported by evidence from ecological studies of *P. syringae*, one of  
310 the most environmentally predominant INA microbial species. However, it should be kept in  
311 mind that precipitation is one of several processes of natural selection that have honed the ice  
312 nucleation activity of this species. The percent of cells of the entire *P. syringae* global population  
313 that actually attains cloud height is unknown and might be very small. Hence, precipitation alone  
314 has probably not been the main driver in the evolution of ice nucleation activity. Nevertheless,  
315 the enrichment of INA *P. syringae* in rain and snowfall compared to its population in clouds

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

316 would be important evidence for the role of this bacterium in the processes leading to  
317 precipitation.

318 *P. syringae* is wide-spread in habitats associated with the cycle of fresh water, from clouds to  
319 precipitation to snow pack, alpine prairies and litter, lakes, rivers, epilithon, and a range of wild  
320 plants as well as crops (Morris *et al.*, 2008, 2010; Monteil *et al.*, 2012). Its populations generally  
321 consist of a mixture of lines of cells of different genotypes and phenotypes, some of which are  
322 INA and others not. However, out of all sources of this bacterium studied, it is only in snowfall –  
323 a form of precipitation that is always initiated by freezing - that all of the strains are markedly  
324 INA at warm temperatures ( $\geq -6^{\circ}\text{C}$ ) (Morris *et al.*, 2008). Furthermore, INA strains of *P.*  
325 *syringae* constitute from 60% to 100% of the populations of this bacterium that fall with rain  
326 (Morris *et al.*, 2013b). These observations reveal a clear enrichment of ice nucleation activity  
327 when compared to the populations in cloud water for which fewer than 10% of strains of this  
328 bacterium are INA (Joly *et al.*, 2013). It should be noted that the regular presence of *P. syringae*  
329 in rain is not likely the result of scrubbing of aerosols below clouds because this process is very  
330 inefficient for particles smaller than several microns in diameter (McDonald, 1962; Respondek *et*  
331 *al.*, 1995). Furthermore, the traits of *P. syringae* strains collected in rainfall above a plant canopy  
332 were distinct from those on the plant canopy indicating that the strains in precipitation came from  
333 a source other than the local plant canopy (Constantinidou *et al.*, 1990). It has been proposed  
334 that, by falling with precipitation, the bacterium avoids a long residence time in the atmosphere  
335 that could lead to death from desiccation or over-exposure to UV (Morris *et al.*, 2013b). Ice  
336 nucleation activity in *P. syringae* is significantly correlated with various other traits allowing it to  
337 grow readily in a wide range of environments (Morris *et al.*, 2010). This capacity would be  
338 necessary for a bacterium that is deposited with precipitation into diverse habitats.



339

340 Interestingly, other species of microorganisms whose life cycle depends critically on air-borne  
341 dissemination and deposition via rainfall, obligate parasitic rust fungi such as *Puccinia* spp. and  
342 *Hemileia vastratrix*, have recently been shown to be highly INA (Morris *et al.*, 2012). Dry  
343 deposition of rust spores rarely occurs once the spores have been transported up to several  
344 hundred meters. Fallout from the atmosphere is assured by rainfall (Nagarajan & Singh, 1990).  
345 In contrast, none of the microorganisms that are dominant in the atmosphere have been shown to  
346 be ice nucleation active at temperatures  $>-10^{\circ}$  C (Mortazavi *et al.*, 2008; Bowers *et al.*, 2009;  
347 Iannone *et al.*, 2011). These observations are strong arguments for the positive selection of  
348 precipitation on ice nucleation activity of certain microorganisms. The ensemble of processes that  
349 are forces for positive natural selection of microbial ice nucleation activity contribute to the  
350 capacity of these microorganisms to participate in a bioprecipitation feedback cycle. If processes  
351 other than precipitation are the main forces for positive selection of ice nucleation activity, then  
352 environmental changes that markedly affect these processes could alter the availability of  
353 microbial ice nuclei and subsequently the bioprecipitation cycle.

354

### 355 **Landscapes, aerosols and phenomena coherent with bioprecipitation**

356 Earth's land masses are the primary source of microbial aerosols in the atmosphere. Based on a  
357 broad literature survey and numerical simulations using a global climate model, the average  
358 emission rate of bacteria over land is about  $200 \text{ m}^{-2} \text{ s}^{-1}$  (Burrows *et al.*, 2009). These emission  
359 rates are consistent with simulated and observed atmospheric number concentrations of bacteria-  
360 containing particles in the range of  $10^4-10^5 \text{ m}^{-3}$  over most continental regions. Emission rates  
361 and average atmospheric concentrations for fungal spores are estimated to be on the same order

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

362 of magnitude (Elbert *et al.*, 2007; Sesartic & Dallafior, 2011; Huffman *et al.*, 2012; Despres et  
363 al., 2013). Vegetation is implicated as the main source of air-borne microorganisms, and more so  
364 than bare soil (Lindemann *et al.*, 1982; Lighthart, 1997; Burrows *et al.*, 2009). In a study of the  
365 composition of hailstones, the culturable bacterial community was skewed toward groups of  
366 bacteria most common on plants, whereas their dissolved organic matter content was mainly from  
367 soils (vs. plants) (Šantl-Temkiv *et al.*, 2013). Overall, concentrations of bacteria and other  
368 bioaerosols are generally much lower over aquatic environments than above terrestrial ones  
369 (Burrows *et al.*, 2009). Furthermore, vegetated land masses are stronger sources of biological  
370 ice nuclei than water masses and non-vegetated regions (Christner *et al.*, 2008). Likewise, clouds  
371 that are warmer than  $-10^{\circ}$  C contain ice more frequently when they are over vegetated continental  
372 regions than at coastal stations or over the open ocean (Kanitz *et al.*, 2011) suggesting that  
373 biological ice nuclei, possessing the unique capacity to catalyze ice formation at these  
374 temperatures, are responsible for this ice formation.

375 The specific mechanisms involved in the emissions of microbial particles into the atmosphere  
376 from their sources are mostly unknown. Some mechanisms, for example, involving active  
377 emissions from dry and wet surfaces have been well documented for fungi. Active release is  
378 prevalent, however, among fungi in only certain species in a limited number of phyla (Meridith,  
379 1973; Elbert *et al.*, 2007). For bacteria and also for a wide range of fungi that do not deploy  
380 active release of spores, the processes of emission are linked mainly to the physical conditions  
381 providing the forces for removal and release of particles. This involves energy input from an  
382 external source provided by wind shear, convection, rain splash, agricultural practices such as  
383 combining, etc. (Upper & Hirano, 1991; Jones & Harrison, 2004). Bacterial launch, in particular,  
384 is most efficient during rain, when droplets shake leaves and release poorly attached particles  
385 (Upper & Hirano, 1991), or at mid-day, when leaves are dry and solar heating promotes

386 convection (Lindemann *et al.*, 1982). Evidence exists for meteorological correlation between  
387 bacterial concentrations and atmospheric conditions (e.g. wind-speed and temperature) (Jones &  
388 Harrison, 2004; Harrison *et al.*, 2005). Although there is much that remains to be revealed about  
389 the specific mechanisms of emission, land use practices have been implicated in the rates of  
390 emission. One influential factor is the type of crop cover which not only influences the rate of  
391 emissions (Lindemann *et al.*, 1982) but clearly influences the diversity of microorganisms that  
392 can potentially be emitted into the atmosphere. Another markedly important factor is harvesting  
393 of a crop (Lighthart, 1997) which can be responsible for the release of up to  $10^{13}$  spores of the  
394 wheat rust fungus, for example, for every 5 ha of slightly diseased wheat that are harvested with a  
395 combine tractor (Friesen *et al.*, 2001).

396 In light of the variability in the abundance of INA microbial populations on different plant  
397 species and in different types of vegetated ecosystems, and of the effect of land use practices on  
398 their emission, it is reasonable to suspect that the marked changes in regional precipitation  
399 patterns over the last century have been partly affected by changes in emission patterns of  
400 microbial ice nuclei resulting from drastic human-induced land use changes over this same  
401 timescale (Lioubimtseva *et al.*, 2005; Raddatz, 2007; Pielke *et al.*, 2007; Zeng & Yoon, 2009;  
402 DeAngelis *et al.*, 2010).

403

### 404 **Future scenarios: changing landscapes, changing rainfall.**

405 Land use changes constitute inadvertent interventions to the bioprecipitation cycle. Alterations to  
406 type, density and seasonality of vegetation cover can severely change the potential source of  
407 biological ice nucleators emitted into the atmosphere (Hirano & Upper, 2000) and thus the  
408 patterns of cloud extent and precipitation downwind. This, in turn, must affect the net fluxes of

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

409 radiation entering the top of the atmosphere and reaching the ground, with possible effects on the  
410 regional climate. A shift in land use often affects soil moisture and modifies heat, moisture and  
411 momentum transfer to the atmosphere with consequences for local and regional weather  
412 (Raddatz, 2007). Large areas subjected to land use change constitute islands on a continental  
413 surface that leave an atmospheric imprint upon the more nearly uniform background surrounding  
414 them. If this imprint could be broken down into all factors causing it, the effect of biological ice  
415 nucleators may become apparent. Three examples indicate where elucidation of feedbacks  
416 involving biological ice nucleators from managed or natural landscapes could contribute to  
417 appraising their impact on regional weather and to (possibly) avoiding nefarious inadvertent  
418 consequences.

419 A spectacular growth during the second half of the 20<sup>th</sup> century in irrigated areas in Central Asia  
420 has significantly increased local precipitation in large oases (Lioubimtseva *et al.*, 2005). Similar  
421 growth in the irrigated area of the American Great Plains has, since its establishment in the early  
422 20<sup>th</sup> century, increased downwind precipitation during the month of July by 15-30 %. Only part  
423 of the additional precipitation can be explained by the increased moisture contributed by  
424 irrigation (DeAngelis *et al.*, 2010). The addition of irrigation not only changes the type of crop  
425 cover, its density and seasonality, it also changes the emission of biological ice nucleators. Yet,  
426 the contribution of crop irrigation to altered regional precipitation patterns is unknown, and has  
427 not been the subject of much research.

428 There have also been land use changes over large areas on the fringes of the major deserts  
429 subjected to overgrazing, where vegetation cover is reduced, desertification progresses, albedo  
430 increases, and evaporation declines. This change leads to a feed-back loop involving a loss of  
431 water vapor from evapotranspiration, where loss of vegetation cover and reduction in

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

432 precipitation reinforce each other (Zeng & Yoon, 2009). But INA microbial aerosols are also  
433 potentially being lost as vegetation declines, and their loss could further accelerate desert  
434 expansion.

435 A third example is the effect of urbanization on atmospheric processes. Urban areas, heat islands  
436 with increased surface roughness, enhance local convection and are also significant sources of  
437 aerosols. Combined, these effects result in more frequent and persistent thunderstorm activity  
438 above large cities, compared to surrounding regions (Ashley *et al.*, 2011). Recent modeling of  
439 thunderstorms over São Paulo City indicates a potentially significant role of biological ice  
440 nucleators in cloud development over the cityscape (Gonçalves *et al.*, 2012). Consequently,  
441 damage caused by hail or flooding could potentially be reduced by modifying the sources of  
442 biological ice nucleators from a cityscape by planting, for example, trees that harbor and release  
443 sufficient populations of microbial ice nucleators.

444 In all three examples, human activities have visible effects on local or regional weather regimes.  
445 As anthropogenic activity and climate change further alter vegetated landscapes, increasingly  
446 extreme repercussions to weather are expected. In weather processes, physical aspects are studied  
447 most intensively. More recently, the role of vegetation is also being considered. Although the  
448 potential of biological ice nucleators to modify cloud development has been the subject of  
449 numerous investigations (e.g. Phillips *et al.*, 2009; Gonçalves *et al.*, 2012), we still lack the first  
450 example of a study linking physical, biological and microbiological effects of human activity,  
451 such as land use change, on changes in regional weather pattern. This begs for concerted  
452 interdisciplinary research on this intersection between microbiology, climatology and land use  
453 ecology to elucidate the extent to which microorganisms drive yet another biogeochemical cycle.

454

455 **References:**

- 456 Agrios GN (2005) *Plant Pathology*. Amsterdam, Academic Press, Elsevier.
- 457 Amato P, Parazols M, Sancelme M, Laj P, Mailhot G, Delort A-M (2007) Microorganisms  
458 isolated from the water phase of tropospheric clouds at the Puy de Dôme: major groups and  
459 growth abilities at low temperatures. *Fems Microbiology Ecology*, **59**, 242–254.
- 460 Ansmann A, Tesche M, Althausen D, *et al.* (2008) Influence of Saharan dust on cloud glaciation  
461 in southern Morocco during the Saharan Mineral Dust Experiment. *Journal of Geophysical*  
462 *Research*, **113**, D04210.
- 463 Ashley WS, Bentley ML, Stallins JA (2011) Urban-induced thunderstorm modification in the  
464 Southeast United States. *Climatic Change*, **113**, 481–498.
- 465 Attard E, Yang H, Delort A-M, *et al.* (2012) Effects of atmospheric conditions on ice nucleation  
466 activity of *Pseudomonas*. *Atmospheric Chemistry and Physics*, **12**, 10667–10677.
- 467 Bates TS, Lamb BK, Guenther A, Dignon J, Stoiber RE (1992) Sulfur emissions to the  
468 atmosphere from natural sources. *Journal of Atmospheric Chemistry*, **14**, 315–337.
- 469 Battistuzzi FU, Feijao A, Hedges SB (2004) A genomic timescale of prokaryote evolution:  
470 insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BMC*  
471 *Evolutionary Biology*, **4**, 44.
- 472 Bigg EK (1958) A long period fluctuation in freezing nucleus concentrations. *Journal of*  
473 *Meteorology*, **15**, 561–562.
- 474 Bower K, Moss S, Johnson D, *et al.* (1996) A parametrization of the ice water content observed  
475 in frontal and convective clouds. *Quarterly Journal of the Royal Meteorological Society*,  
476 **122**, 1815–1844.
- 477 Bowers RM, Lauber CL, Wiedinmyer C, *et al.* (2009) Characterization of airborne microbial  
478 communities at a high-elevation site and their potential to act as atmospheric ice nuclei.  
479 *Applied and Environmental Microbiology*, **75**, 5121–5130.
- 480 Bowers RM, McLetchie S, Knight R, Fierer N (2011) Spatial variability in airborne bacterial  
481 communities across land-use types and their relationship to the bacterial communities of  
482 potential source environments. *The ISME journal*, **5**, 601–12.
- 483 Burrows SM, Butler T, Jöckel P, Tost H, Kerkweg A, Pöschl U, Lawrence MG (2009) Bacteria  
484 in the global atmosphere – Part 2: Modeling of emissions and transport between different  
485 ecosystems. *Atmospheric Chemistry and Physics*, **9**, 9281–9297.

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-351. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

- 486 Christner BC, Morris CE, Foreman CM, Cai R, Sands DC (2008) Ubiquity of biological ice  
487 nucleators in snowfall. *Science*, **319**, 1214.
- 488 Conen F, Morris CE, Leifeld J, Yakutin MV, Alewell C (2011). Biological residues define the ice  
489 nucleation properties of soil dust. *Atmosphere Chemistry and Physics*, 11:9643-9648  
490 doi:10.5194/acp-11-9643-2011, 2011.
- 491 Conrad R (2009) The global methane cycle: recent advances in understanding the microbial  
492 processes involved. *Environmental Microbiology Reports*, **1**, 285–292.
- 493 Constantinidou HA, Hirano SS, Baker LS, Upper CD (1990) Atmospheric dispersal of ice  
494 nucleation-active bacteria : the role of rain. *Phytopathology*, **80**, 934–937.
- 495 D’Souza NA, Kawaraski Y, Gantz JD, *et al.* (2013) Diatom assemblages promote ice formation  
496 in large lakes. *ISME Journal*, **7**, 1632–1640.
- 497 DeAngelis A, Dominguez F, Fan Y, Robock A, Kustu MD, Robinson D (2010) Evidence of  
498 enhanced precipitation due to irrigation over the Great Plains of the United States. *Journal*  
499 *of Geophysical Research*, **115**, 1–14.
- 500 DeConto RM (2008) Plate tectonics and climate change. In: *Encyclopedia of Paleoclimatology*  
501 *and Ancient Environments* (eds: Gornitz V), pp784–797. Dordrecht, Springer-Verlag.
- 502 DeMott PJ (1990) An exploratory study of ice nucleation on soot aerosols. *J. Appl. Meteorol.*, **29**,  
503 1072–1079.
- 504 DeMott PJ, Cziczo DJ, Prenni AJ, *et al.* (2003) Measurements of the concentration and  
505 composition of nuclei for cirrus formation. *Proceedings of the National Academy of*  
506 *Sciences*, **100**, 14655–14660.
- 507 DeMott PJ, Möhler O, Stetzer O, *et al.* (2011) Resurgence in ice nuclei measurement research.  
508 *Bulletin of the American Meteorological Society*, **92**, 1623–1635.
- 509 DeMott PJ, Prenni AJ (2010) New Directions: Need for defining the numbers and sources of  
510 biological aerosols acting as ice nuclei. *Atmospheric Environment*, **44**, 1944–1945.
- 511 Despres VR, Huffman JA, Burrows SM, Hoose C, Safatov AS, Buryak GA, Fröhlich-Nowoisky  
512 J, Elbert W, Andreae MO, Pöschl U, and Jaenicke R (2012) Primary biological aerosol  
513 particles in the atmosphere: A review. *Tellus B*, **64**, 15598, doi:10.3402/tellusb.v64i0.15598.
- 514 Elbert W, Taylor PE, Andreae MO, Pöschl U (2007) Contribution of fungi to primary biogenic  
515 aerosols in the atmosphere: wet and dry discharged spores, carbohydrates, and inorganic  
516 ions. *Atmospheric Chemistry and Physics*, **7**, 4569–4588.

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

- 517 Fahy GM (1995) The role of nucleation in cryopreservation. In: *Biological Ice Nucleation and Its*  
518 *Applications* (eds: Lee RJ, Warren GJ, Gusta L V), pp315–336. St. Paul, MN, USA, APS  
519 Press.
- 520 Fall R, Schnell RC (1985) Association of an ice-nucleating pseudomonad with cultures of the  
521 marine dinoflagellate, *Heterocapsa niei*. *Journal of Marine Research*, **43**, 257–265.
- 522 Foreman CM, Cory RM, Morris CE, *et al.* (2013) Microbial growth under humic-free conditions  
523 in a supraglacial stream system on the Cotton Glacier, Antarctica. *Environmental Research*  
524 *Letters*, **8**, 035022 doi:10.1088/1748–9326/8/3/035022.
- 525 Freeman BC, Beattie GA (2009) Bacterial growth restriction during host resistance to  
526 *Pseudomonas syringae* is associated with leaf water loss and localized cessation of vascular  
527 activity in *Arabidopsis thaliana*. *Molecular Plant Microbe Interactions*, **22**, 857–67.
- 528 Friesen TL, de Wolf ED, Frankl LJ (2001) Source strength of wheat pathogens during combine  
529 harvest. *Aerobiologia*, **17**, 293–299.
- 530 Garcia E, Hill TC., Prenni AJ, DeMott PJ, Franc GD, Kreidenweis SM (2012) Biogenic ice  
531 nuclei in boundary layer air over two U.S. High Plains agricultural regions. *Journal of*  
532 *Geophysical Research*, **doi:10.102**.
- 533 Gonçalves FLT, Martins JA, Albrecht RI, Morales CA, Silva Dias MA, Morris CE (2012) Effect  
534 of bacterial ice nuclei on the frequency and intensity of lightning activity inferred by the  
535 BRAMS model. *Atmospheric Chemistry and Physics*, **13**, 5677–5689.
- 536 Hahn CJ, Rossow WB, Warren SG (2001) ISCCP cloud properties associated with standard cloud  
537 types identified in individual surface observations. *Journal of Climate*, **14**, 11–28.
- 538 Hallett J, Mossop SC (1974) Production of secondary ice particles during the riming process.  
539 *Nature*, **249**, 26–28.
- 540 Harris-Hobbs RL, Cooper WA (1987) Field evidence supporting quantitative predictions of  
541 secondary ice production rates. *Journal of Atmospheric Science*, **44**, 1071–1082.
- 542 Harrison RM, Jones AM, Biggins PDE, *et al.* (2005) Climate factors influencing bacterial count  
543 in background air samples. *Int. J. Biometeorol.*, **49**, 167–178.
- 544 Hirano SS, Baker LS, Upper CD (1996) Raindrop momentum triggers growth of leaf-associated  
545 populations of *Pseudomonas syringae* on field-grown snap bean plants. *Applied and*  
546 *Environmental Microbiology*, **62**, 2560–2566.
- 547 Hirano SS, Upper CD (2000) Bacteria in the leaf ecosystem with emphasis on *Pseudomonas*  
548 *syringae*-a pathogen, ice nucleus, and epiphyte. *Microbiology and Molecular Biology*  
549 *Reviews*, **64**, 624–653.



- 550 Hirst JM, Stedman OJ, Hogg WH (1967) Long-distance spore transport : Methods of  
551 measurement, vertical spore profiles and the detection of immigrant spores. *Journal of*  
552 *General Microbiology*, **487**, 329–355.
- 553 Hoose C, Kristjánsson JE, Burrows SM (2010) How important is biological ice nucleation in  
554 clouds on a global scale? *Environmental Research Letters*, **5**, 024009.
- 555 Huffman JA, Pöhlker C, Prenni AJ, *et al.* (2013) High concentrations of biological aerosol  
556 particles and ice nuclei during and after rain. *Atmospheric Chemistry and Physics*, **13**, 1767–  
557 1793.
- 558 Huffman JA, Sinha B, Garland RM, *et al.* (2012) Size distributions and temporal variations of  
559 biological aerosol particles in the Amazon rainforest characterized by microscopy and real-  
560 time UV-APS fluorescence techniques during AMAZE-08. *Atmospheric Chemistry and*  
561 *Physics*, **12**, 11997–12019.
- 562 Iannone R, Chernoff DI, Pringle A, Martin ST, Bertram AK (2011) The ice nucleation ability of  
563 one of the most abundant types of fungal spores found in the atmosphere. *Atmospheric*  
564 *Chemistry and Physics*, **11**, 1191–1201.
- 565 Joly M, Attard E, Sancelme M, *et al.* (2013) Ice nucleation activity of bacteria isolated from  
566 cloud water. *Atmospheric Environment*, **70**, 392–400.
- 567 Jones AM, Harrison RM (2004) The effects of meteorological factors on atmospheric bioaerosol  
568 concentrations--a review. *Science of the Total Environment*, **326**, 151–180.
- 569 Kajava A V. (1995) Molecular modeling of the three-dimensional structure of bacterial in  
570 proteins. In: *Biological Ice Nucleation and its Applications*. (eds: Lee Jr. RE, Warren GJ,  
571 Gusta L V), pp101–114. St. Paul, APS Press.
- 572 Kanitz T, Seifert P, Ansmann A, Engelmann R, Althausen D, Casiccia C, Rohwer EG (2011)  
573 Contrasting the impact of aerosols at northern and southern midlatitudes on heterogeneous  
574 ice formation. *Geophys. Res. Lett.*, **38**, 1–5.
- 575 Kasting JF, Siefert JL (2002) Life and the evolution of Earth's atmosphere. *Science*, **296**, 1066–  
576 1068.
- 577 Lerat E, Daubin V, Moran NA (2003) From gene trees to organismal phylogeny in prokaryotes:  
578 the case of the gamma-Proteobacteria. *PLoS Biology*, **1**, E19.
- 579 Lighthart B (1997) The ecology of bacteria in the alfresco atmosphere. *FEMS Microbiology*  
580 *Ecology*, **23**, 263–274.
- 581 Lindemann J, Constantinidiou HA, Barchet WR, Upper CD (1982) Plants as source of airborne  
582 bacteria, including ice nucleation-active bacteria. *Applied and Environmental Microbiology*,  
583 **44**, 1059–1063.

- 584 Lioubimtseva E, Cole R, Adams JM, Kapustin G (2005) Impacts of climate and land-cover  
585 changes in arid lands of Central Asia. *Journal of Arid Environments*, **62**, 285–308.
- 586 McDonald JE (1962) Collection and washout of airborne pollens and spores by raindrops.  
587 *Science*, **135**, 435–437.
- 588 Meridith DS (1973) Significance of spore release and dispersal mechanisms in plant disease  
589 epidemiology. *Annual Review of Phytopathology*, **11**, 313–342.
- 590 Möhler O, Demott PJ, Vali G, Levin Z (2007) Microbiology and atmospheric processes: the role  
591 of biological particles in cloud physics. *Biogeosciences*, **4**, 1059–1071.
- 592 Möhler O, Georgakopoulos DG, Morris CE, *et al.* (2008) Heterogeneous ice nucleation activity  
593 of bacteria: new laboratory experiments at simulated cloud conditions. *Biogeosciences*, **5**,  
594 1435–1445.
- 595 Monteil CL, Guilbaud C, Glaux C, Lafolie F, Soubeyrand S, Morris CE (2012) Emigration of the  
596 plant pathogen *Pseudomonas syringae* from leaf litter contributes to its population dynamics  
597 in alpine snowpack. *Environmental Microbiology*, **14**, 2099–2112.
- 598 Morris CE, Georgakopoulos DG, Sands DC (2004) Ice nucleation active bacteria and their  
599 potential role in precipitation. *Journal of Physics IV, France*, **121**, 87–103.
- 600 Morris CE, Leyronas C, Nicot PC (2013a) Movement of bioaerosols in the atmosphere and its  
601 consequences on climate and microbial evolution. In: *Aerosol Science: Technology and*  
602 *Applications* (eds: Colbeck, I.; Mihalis L), Hoboken, NJ, John Wiley & Sons, *in press*.
- 603 Morris CE, Monteil CL, Berge O (2013b) The life history of *Pseudomonas syringae*: Linking  
604 agriculture to Earth system processes. *Annual Review of Phytopathology*, **51**, 85-104.
- 605 Morris CE, Sands DC, Bardin M, *et al.* (2011) Microbiology and atmospheric processes: research  
606 challenges concerning the impact of airborne micro-organisms on the atmosphere and  
607 climate. *Biogeosciences*, **8**, 17–25.
- 608 Morris CE, Sands DC, Glaux C, *et al.* (2012) Urediospores of rust fungi are ice nucleation active  
609 at > -10 °C and harbor ice nucleation active bacteria. *Atmospheric Chemistry and Physics*,  
610 **13**, 4223–4233.
- 611 Morris CE, Sands DC, Vanneste JL, Montarry J, Oakley B, Guilbaud C, Glaux C (2010) Inferring  
612 the evolutionary history of the plant pathogen *Pseudomonas syringae* from its biogeography  
613 in headwaters of rivers in North America, Europe and New Zealand. *mBio*, **1**, e00107–10–  
614 e00107–20.
- 615 Morris CE, Sands DC, Vinatzer BA, *et al.* (2008) The life history of the plant pathogen  
616 *Pseudomonas syringae* is linked to the water cycle. *ISME Journal*, **2**, 321–334.

- 617 Mortazavi R, Hayes CT, Ariya PA (2008) Ice nucleation activity of bacteria isolated from snow  
618 compared with organic and inorganic substrates. *Environmental Chemistry*, **5**, 373–381.
- 619 Mossop SC (1963) Atmospheric ice nuclei. *Zeitschrift für angewandte Mathematik und Physik*,  
620 **14**, 456–486.
- 621 Murray BJ, Broadley SL, Wilson TW, Bull SJ, Wills RH, Christenson HK, Murray EJ (2010)  
622 Kinetics of the homogeneous freezing of water. *Physical Chemistry Chemical Physics*, **12**,  
623 10380–10387.
- 624 Murray BJ, Knopf DA, Bertram AK (2005) The formation of cubic ice under conditions relevant  
625 to Earth’s atmosphere. *Nature*, **434**, 202–205.
- 626 Murray BJ, O’Sullivan D, Atkinson JD, Webb ME (2012) Ice nucleation by particles immersed  
627 in supercooled cloud droplets. *Chemical Society Reviews*, **41**, 6519–6554.
- 628 Nagarajan S, Singh DV (1990) Long-distance dispersion of rust pathogens. *Annual Review of*  
629 *Phytopathology*, **28**, 139–153.
- 630 Nielsen R (2005) Molecular signatures of natural selection. (WL Montgomery, Ed.). *Annual*  
631 *Review of Genetics*, **39**, 197–218.
- 632 O’Sullivan D, Murray BJ, Malkin T., Whale T, Umo NS, Atkinson, JD, Price HC, Baustian KJ,  
633 Browse J, and Webb ME (2013) Ice nucleation by soil dusts: relative importance of mineral  
634 dust and biogenic components. *Atmospheric Chemistry and Physics Discussion*, **13**, 20275-  
635 20317.
- 636 Phillips VTJ, Andronache C, Christner BC, *et al.* (2009) Potential impacts from biological  
637 aerosols on ensembles of continental clouds simulated numerically. *Biogeosciences*, **6**, 1–28.
- 638 Phillips VTJ, Andronache C, Sherwood SC, *et al.* (2005) Anvil glaciation in a deep cumulus  
639 updraught over Florida simulated with the Explicit Microphysics Model. I: Impact of  
640 various nucleation processes. *Quarterly Journal of the Royal Meteorological Society*, **131**,  
641 2019–2046.
- 642 Phillips VTJ, Blyth AM, Brown PRA, Choulaton TW, Latham J (2001) The glaciation of a  
643 cumulus cloud over New Mexico. *Quarterly Journal of the Royal Meteorological Society*,  
644 **127**, 1513–1534.
- 645 Phillips VTJ, Choulaton TW, Illingworth AJ, Hogan RJ, Field PR (2003) Simulations of the  
646 glaciation of a frontal mixed-phase cloud with the Explicit Microphysics Model. *Quarterly*  
647 *Journal of the Royal Meteorological Society*, **129**, 1351–1371.
- 648 Phillips VTJ, DeMott PJ, Andronache C (2008) An empirical parameterization of heterogeneous  
649 ice nucleation for multiple chemical species of aerosol. *Journal of the Atmospheric Sciences*,  
650 **65**, 2757–2783.

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

- 651 Phillips VTJ, Demott PJ, Andronache C, Pratt KA, Prather KA, Subramanian R, Twohy C (2013)  
652 Improvements to an empirical parameterization of heterogeneous ice nucleation and its  
653 comparison with observations. *Journal of the Atmospheric Sciences*, **70**, doi: 10.1175/JAS–  
654 D–12–080.1.
- 655 Pielke RA, Adegoke J, Beltrán-Przekurat A, *et al.* (2007) An overview of regional land-use and  
656 land-cover impacts on rainfall. *Tellus B*, **59**, 587–601.
- 657 Pöschl U, Martin ST, Sinha B, *et al.* (2010) Rainforest aerosols as biogenic nuclei of clouds and  
658 precipitation in the Amazon. *Science*, **329**, 1513–1516.
- 659 Prenni AJ, Petters MD, Kreidenweis SM, *et al.* (2009) Relative roles of biogenic emissions and  
660 Saharan dust as ice nuclei in the Amazon basin. *Nature Geoscience.*, **2**, 402–405.
- 661 Prenni AJ, Tobo Y, Garcia E, *et al.* (2013) The impact of rain on ice nuclei populations at a  
662 forested site in Colorado. *Geophysical Research Letters*, **40**, 227–231.
- 663 Raddatz RL (2007) Evidence for the influence of agriculture on weather and climate through the  
664 transformation and management of vegetation: Illustrated by examples from the Canadian  
665 Prairies. *Agricultural and Forest Meteorology*, **142**, 186–202.
- 666 Reid A (2011) *Incorporating microbial processes into climate models*. American Academy of  
667 Microbiology,  
668 [http://academy.asm.org/images/stories/documents/Incorporating\\_Microbial\\_Processes\\_Into\\_](http://academy.asm.org/images/stories/documents/Incorporating_Microbial_Processes_Into_Climate_Models.pdf)  
669 [Climate\\_Models.pdf](http://academy.asm.org/images/stories/documents/Incorporating_Microbial_Processes_Into_Climate_Models.pdf)
- 670 Respondek PS, Flossmann AI, Alheit RR, Pruppacher HR (1995) A theoretical study of the wet  
671 removal of atmospheric pollutants. 5. The uptake, redistribution, and deposition of  
672 (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> by a convective cloud containing ice. *Journal of the Atmospheric Sciences*, **52**,  
673 2121–2132.
- 674 Rossow WB, Schiffer RA (1999) Advances in Understanding Clouds from ISCCP. *Bulletin of the*  
675 *American Meteorological Society*, **80**, 2261–2287.
- 676 Sands DC, Langhans VE, Scharen AL, de Smet G (1982) The association between bacteria and  
677 rain and possible resultant meteorological implications. *Journal of the Hungarian*  
678 *Meteorological Service*, **86**, 148–152.
- 679 Šantl-Temkiv T, Finster K, Dittman T, Hansen BM, Thyraug R, Nielsen NW, Karlson UG  
680 (2013) Hailstones: A window into the microbial and chemical inventory of a storm cloud.  
681 *PLoS ONE*, **8**, e53550.
- 682 Sesartic A, Dallafior TN (2011) Global fungal spore emissions, review and synthesis of literature  
683 data. *Biogeosciences*, **8**, 1181–1192.

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

- 684 Szyrmer W, Zawadzki I (1997) Biogenic and anthropogenic sources of ice-forming nuclei: A  
685 review. *Bulletin of the American Meteorological Society*, **78**, 209–228.
- 686 Tobo Y, Prenni AJ, DeMott PJ, Huffman JA, McCluskey CS, Tian G, Pöhlker C, Pöschl U,  
687 Kreidenweis SM (2013) Biological aerosol particles as a key determinant of ice nuclei  
688 populations in a forest ecosystem, *Journal of Geophysical Research. Atmospheres* **118**,  
689 doi:[10.1002/jgrd.50801](#).
- 690 Upper CD, Hirano SS (1991) Aerial dispersal of bacteria. *Biotechnology (Reading Mass.)*, **15**,  
691 75–93.
- 692 Wolber PK (1993) Bacterial ice nucleation. *Adv. Microb. Physiol.*, **34**, 203–237.
- 693 Zachariassen KE, Kristiansen E (2000) Ice nucleation and antinucleation in nature. *Cryobiology*,  
694 **41**, 257–79.
- 695 Zeng N, Yoon J (2009) Expansion of the world's deserts due to vegetation-albedo feedback under  
696 global warming. *Geophysical Research Letters*, **36**.
- 697 Zhou J, Poulsen CJ, Rosenbloom N, Shields C, Briegleb B (2012) Vegetation-climate  
698 interactions in the warm mid-Cretaceous. *Climate of the Past*, **8**, 565–576.
- 699
- 700

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

701

702 **Acknowledgments:** The authors thank the Epicurus Fund at DonorsTrust for funding to cover  
703 travel for authors to meet. J. A. H. acknowledges internal faculty funding from the University of  
704 Denver. V. P. acknowledges support from US Department of Energy's BER program for an  
705 award supporting modeling research into aerosol impacts on glaciated clouds. C.E.M. thanks the  
706 US NSF Division of Atmospheric and Geospace Sciences for funding to stimulate scientific  
707 communication on the interaction of bioaerosols with atmospheric processes.

708

709 **Author contributions:** All authors contributed to the conception and writing of this paper. They  
710 are all aware of the full contents and give their consent to its publication.

711

712 **The authors declare no conflict of interest**

713

714 **Figure legends**

715

716 **Figure 1.** Environmental phenomena contributing to the bioprecipitation cycle. There are two  
717 essential components of bioprecipitation: i) water vapor (blue lines) and ice nucleation active  
718 (INA) microorganisms (orange lines) are emitted from plants into the atmosphere where they  
719 participate in the process leading to rain and snowfall and ii) the resulting precipitation (direct  
720 rainfall or snow melt that feeds into groundwater) enhances the growth of plants and  
721 microorganisms. Plants are the major source of INA microorganisms in the atmosphere. This is  
722 reflected in the greater abundance of ice nuclei active at temperatures  $>-10^{\circ}\text{C}$ , typical of  
723 microbial ice nuclei, over vegetated land masses than over oceans and is coherent with  
724 phenomena involved in the bioprecipitation cycle. Ice nucleation activity of microorganisms is  
725 positively selected in various ecosystems and environmental contexts (dotted lines) including  
726 aquatic habitats where freezing occurs, on frost damaged plants and with precipitation itself.  
727 These phenomena ensure the positive evolution of ice nucleation activity in certain  
728 microorganisms and provide a favorable context for bioprecipitation.

729

730 **Figure 2.** Evolution of ice nucleation active (INA) bacteria in the timeline of Earth's history.  
731 The bacterial ice nucleation protein originated from a common ancestor of the  $\gamma$ -Proteobacteria, a  
732 class of bacteria that emerged about 1.75 billion years ago (Gya). This group of bacteria  
733 witnessed about 250 million years of glaciation (blue periods in the temperature bar) before the  
734 colonization of land by higher plants. Ice nucleation activity was advantageous most probably  
735 due to the latent heat released during freezing thereby enhancing survival in cold aquatic habitats  
736 before landmasses were inhabitable. After their association with land plants, INA bacteria were

## Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](#).

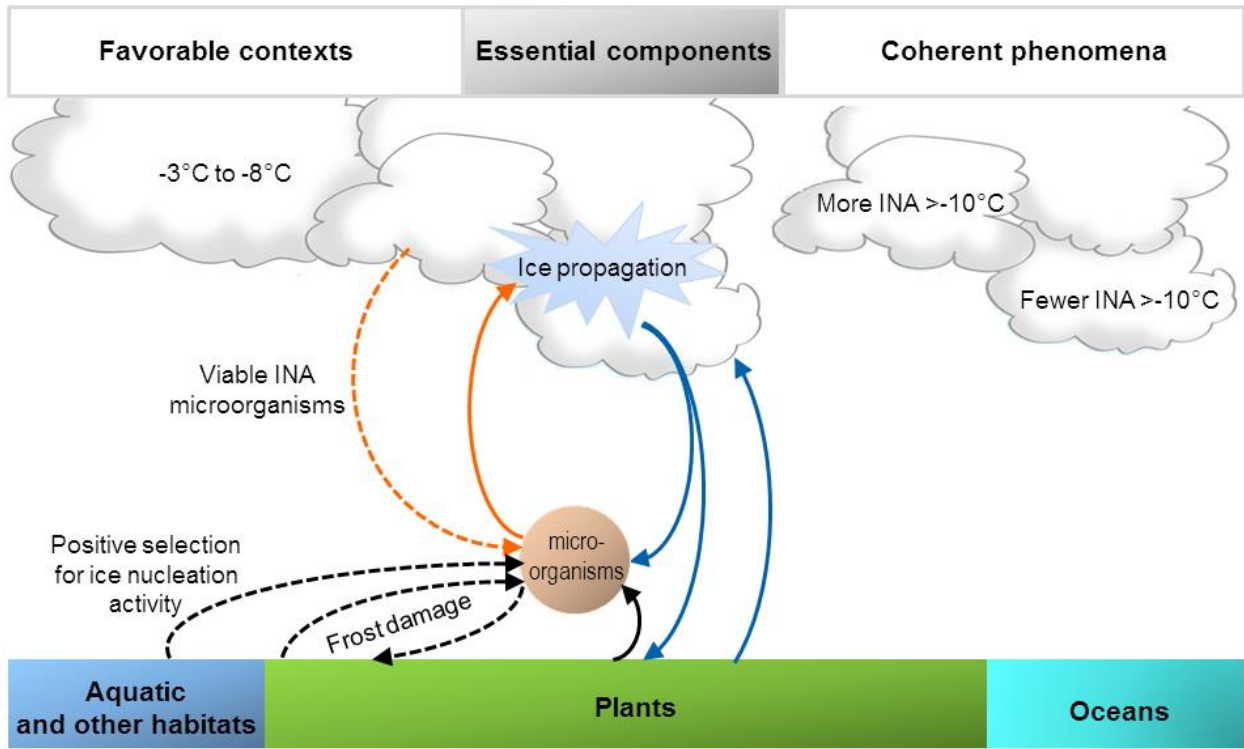
737 readily swept up into the atmosphere and into clouds. The cycle of aerosols of INA bacteria from  
738 modern landscapes being washed back to Earth's surface with precipitation represents a process  
739 that has been occurring since at least the time of instauration of modern atmospheric circulation  
740 patterns and cloud formation (about 100 million years) and is facilitated by a protein with several  
741 hundred million more years of history of interaction with ice.  
742



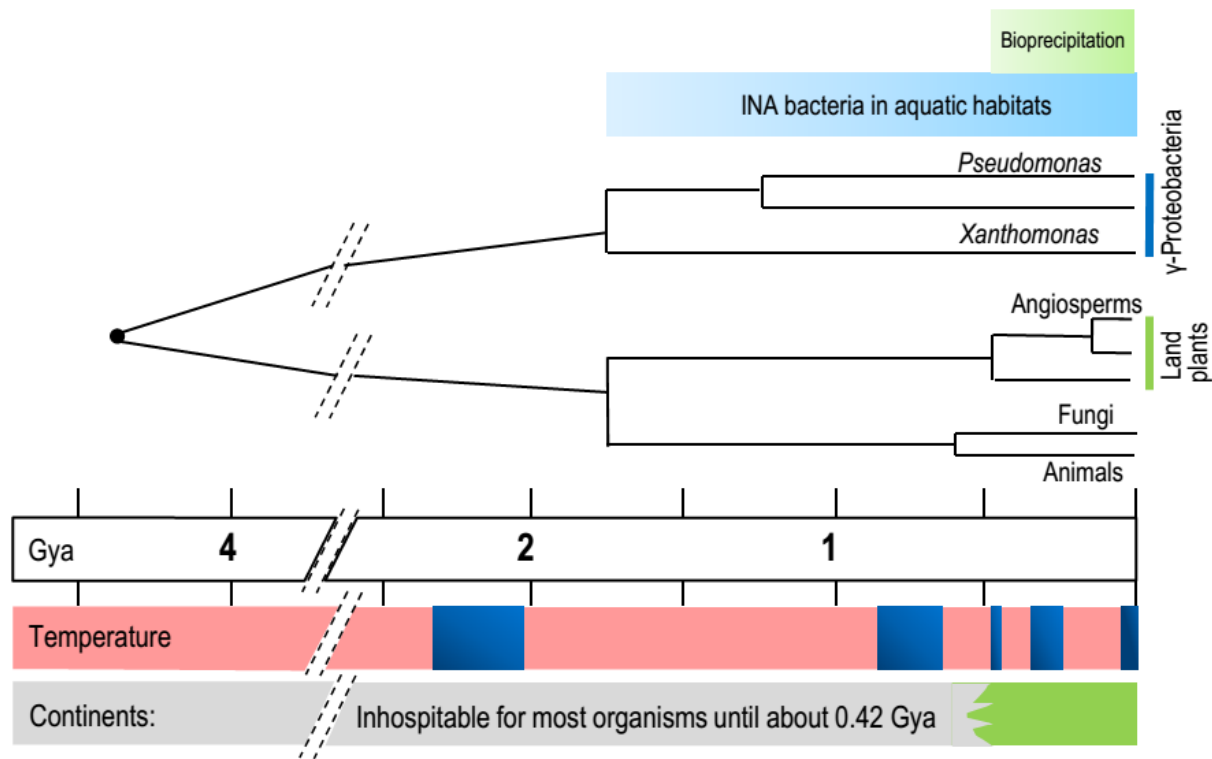
# Postprint

Version définitive du manuscrit publié dans / Final version of the manuscript published in *Global Change Biology*, 2014, 20 (2), 341-51. DOI : 10.1111/gcb.12447. The original publication is available at [Wiley Online library](http://Wiley Online library).

743 Figure 1.  
744



745  
746  
747 Figure 2.  
748



749