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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

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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.

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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 O₂ 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

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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

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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 (≥ 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

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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

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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

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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°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°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

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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 cells m^{-3} in a snap bean field having on average 2.7×10^6 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 cells L^{-1} . In contrast,
222 using microbiological culture media, Lindemann and colleagues could detect as few as 0.001
223 bacterial cells 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⁻¹. 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

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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 γ -Proteobacteria, suggest that as of the Cretaceous period of Earth's history all of the
254 fundamental conditions were in place for INA γ -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°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 γ -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 γ -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 γ -
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

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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 γ -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 γ -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 γ -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 γ -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 γ -
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.

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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

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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 m^{-3} over most continental regions. Emission rates
361 and average atmospheric concentrations for fungal spores are estimated to be on the same order

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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° 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

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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 20th 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 20th 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

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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

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711

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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 γ -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

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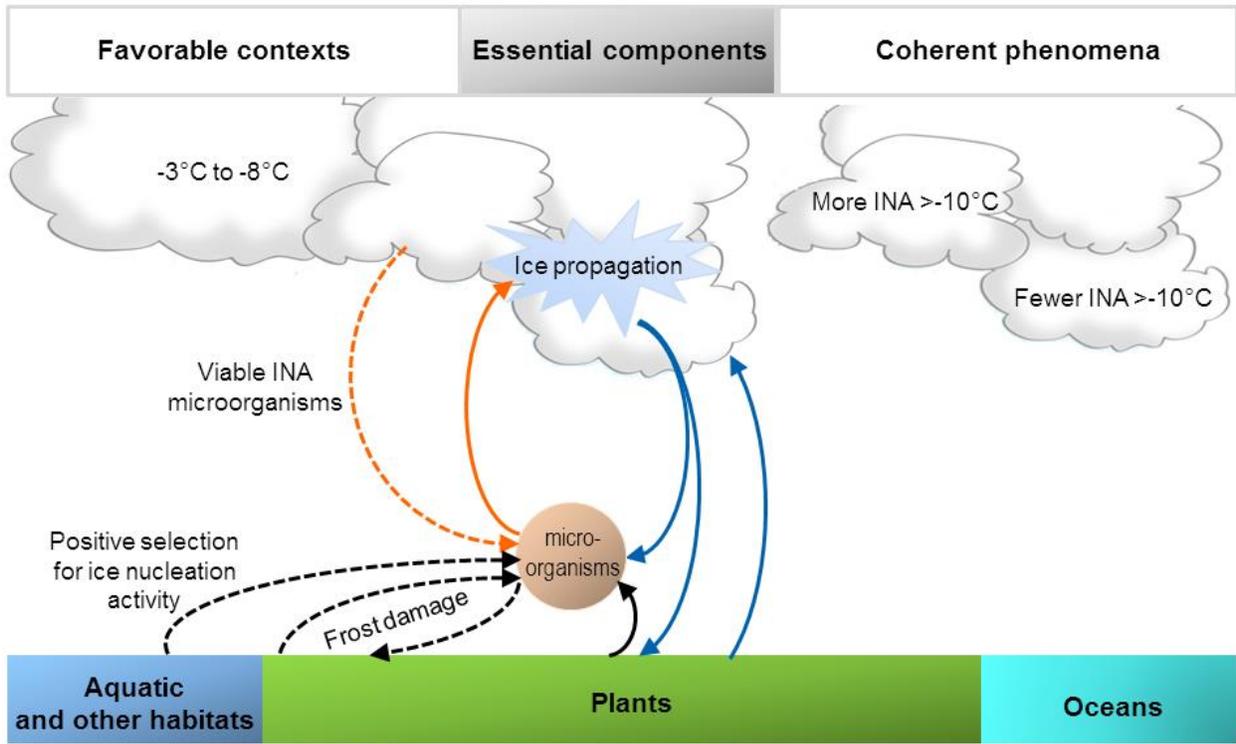
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737 readily swept up into the atmosphere and into clouds. The cycle of aerosols of INA bacteria from
738 modern landscapes being washed back to Earth's surface with precipitation represents a process
739 that has been occurring since at least the time 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.
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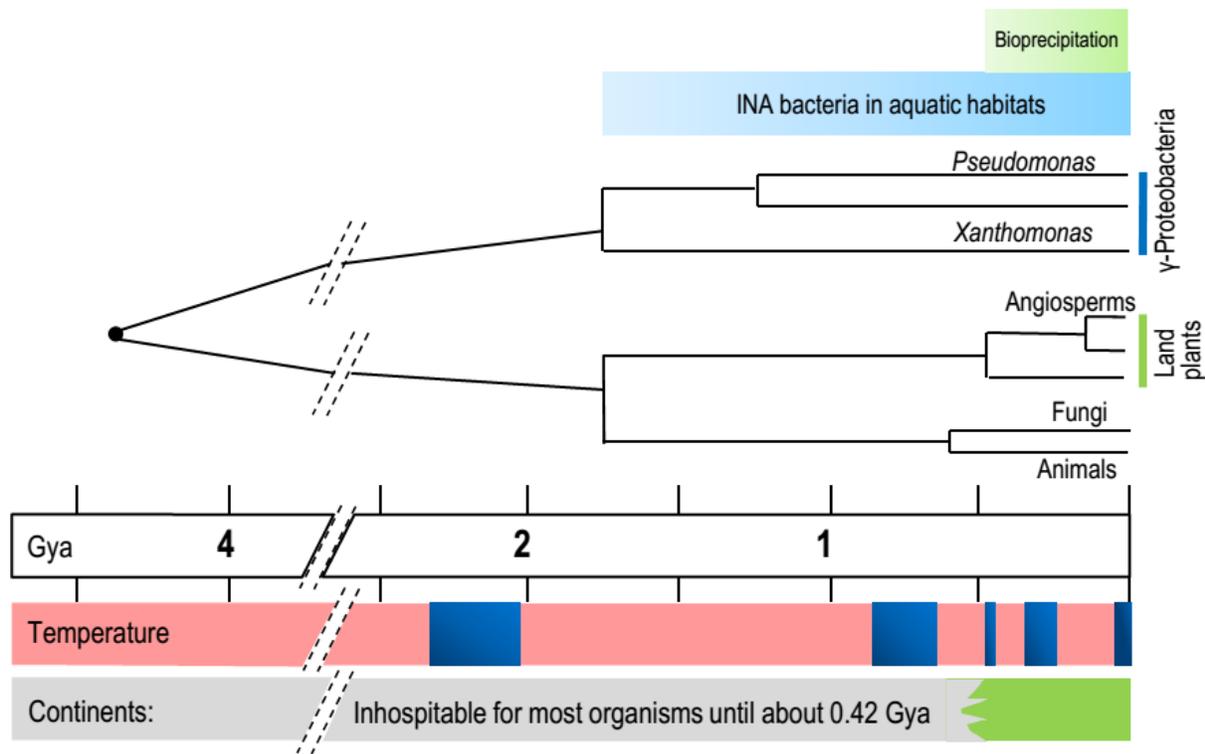
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743 Figure 1.
744



745
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747 Figure 2.
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