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Microbiotic crusts on soil, rock and plants: neglected major players in the global cycles of carbon and nitrogen?

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Abstract

Microbiotic crusts consisting of bacteria, fungi, algae, lichens, and bryophytes colonize most terrestrial surfaces, and they are able to fix carbon and nitrogen from the atmosphere. Here we show that microbiotic crusts are likely to play major roles in the global biogeochemical cycles of carbon and nitrogen, and we suggest that they should be further characterized and taken into account in studies and models of the Earth system and climate.

For the global annual net uptake of carbon by microbiotic crusts we present a first estimate of ~3.6 Pg a^{-1}. This uptake corresponds to ~6% of the estimated global net carbon uptake by terrestrial vegetation (net primary production, NPP: ~60 Pg a^{-1}), and it is of the same magnitude as the global annual carbon turnover due to biomass burning. The estimated rate of nitrogen fixation by microbiotic crusts (~45 Tg a^{-1}) amounts to ~40% of the global estimate of biological nitrogen fixation (107 Tg a^{-1}). With regard to Earth system dynamics and global change, the large contribution of microbiotic crusts to nitrogen fixation is likely to be important also for the sequestration of CO_2 by terrestrial plants (CO_2 fertilization), because the latter is constrained by the availability of fixed nitrogen.

1 Introduction

Microbiotic crusts consisting of bacteria, fungi, algae, lichens, and bryophytes colonize most terrestrial surfaces (Figs. 1 and S1, see http://www.biogeosciences-discuss.net/6/6983/2009/bgd-6-6983-2009-supplement.pdf). In the form of biological soil crusts (BSC) and rock crusts (BRC), they inhabit soils and rocks in arid and semiarid regions as well as in other climatic zones (Friedmann, 1980; Friedmann et al., 1993; Matthes-Sears et al., 1997; Kappen et al., 1998; Büdel, 1999; Kurina and Vitousek, 1999; Zaady et al., 2000; Büdel, 2002; Belnap, 2003; Belnap and Lange, 2003; Rascher et al., 2003; Boison et al., 2004; Hoppert et al., 2004; Walker et al., 2005; Bhatnagar et al., 2008;

Büdel et al., 2008; Schmidt et al., 2008; Weber et al., 2008; Wilske et al., 2008). Microbiotic crusts also cover a large proportion of the surface of terrestrial plants, including stems and branches of trees (epiphytic crusts) as well as tree leaves (epiphyllic crusts) (Ruinen, 1956; Last and Deighton, 1965; Berrie and Eze, 1975; Bentley, 1987; Sheridan, 1991a; Peveling et al., 1992; Coley et al., 1993; Freiberg, 1999; Büdel et al., 2000; Freiberg and Freiberg, 2000; Sillett and Rambo, 2000; Campbell and Coxson, 2001; Lücking and Matzer, 2001; Anthony et al., 2002; Radies and Coxson, 2004; Wanek and Portl, 2005; Lakatos et al., 2006; Cáceres et al., 2007). For the sake of brevity, we shall include both types in the term “epiphytic crusts” (EPC).

It is well known that these communities are able to fix carbon and nitrogen from the atmosphere (Mayland and McIntosh, 1966; Jones, 1970; Bentley, 1987; Beymer and Klopatek, 1991; Lange et al., 1992; Freiberg, 1998; Evans and Johansen, 1999; Juhász et al., 2002; Belnap, 2003; Boison et al., 2004; Yeager et al., 2007). They produce biomass and they release C- and N-containing compounds like carbohydrates and amino acids to the surrounding ecosystem (Boucher and Nash, 1990; Beymer and Klopatek, 1991; Coxson et al., 1992; Belnap and Lange, 2003; Turetsky, 2003; Dojani et al., 2007; Schmidt et al., 2008). However, their contribution to the global cycles of carbon and nitrogen has not yet been quantified. In this study we calculate and present first estimates of the global annual net uptake of CO_2 and fixation of N_2 by microbiotic crusts.

2 Methods

From earlier studies of microbiotic crusts we have compiled as many estimates of annual uptake fluxes and surface coverage values as we could find in a thorough literature search. For global upscaling we used median values of the flux data in combination with global estimates of the surface areas of (semi)arid regions and plants, respectively. All used data and references are tabulated in the Appendix (Tables A1–A9).

Note that we used median rather than arithmetic mean values in order to obtain conservative estimates. The median values were generally in fair agreement with the corresponding arithmetic mean values, and the relative standard errors of the mean values (relative standard deviation divided by the square root of the number of data points) ranged up to ∼80%. Thus we assume that the presented global estimates are uncertain by a factor of ∼2.

3 Results and discussion

For the net uptake of carbon by soil crusts in arid and semi-arid regions, we obtained a median flux of ∼16 $\mathrm{g\,m^{-2}\,a^{-1}}$ (Table A1a). Multiplication with the global dry-land area (Table A2) yields an estimate of ∼1.0 $\mathrm{Pg\,a^{-1}}$ for the net uptake of carbon by BSC in arid and semi-arid regions. With regard to the carbon balance, the reported net uptake values (photosynthesis minus respiration) should be considered as net primary production (NPP) (Chapin et al., 2006).

Soil crusts occur also in non-vegetated gaps of grasslands, tundra and steppe formations, sparsely vegetated grounds of temperate and boreal forests, burnt forest areas, formerly permafrosted soils, and previously ice-covered glacier grounds (Forman and Dowden, 1977; Eversman and Horton, 2004; Schmidt et al., 2008). The median net carbon uptake by soil crusts in these areas is ∼23 $\mathrm{g\,m^{-2}\,a^{-1}}$ (Table A1b), and that by rock crusts is ∼8 $\mathrm{g\,m^{-2}\,a^{-1}}$ (Table A1c). Because the global area colonized by non-arid BSC and by rock crusts are not known, we cannot provide a quantitative estimate for their carbon uptake, but obviously any non-zero flux will increase the total amount of carbon taken up by biological crusts to more than the value of ∼1 $\mathrm{Pg\,a^{-1}}$ given above for arid and semiarid soil crusts alone.

For the net uptake of carbon by epiphytic crusts, we obtained a median flux of ∼28 $\mathrm{g\,m^{-2}\,a^{-1}}$ (Table A3). Multiplication with the corresponding global surface areas of evergreen leaves, branches and stems of trees, and tropical lianas (Tables A4, A5, and A7), assuming coverages of 30–50% (Tables A6 and A7), yields an estimate of ∼2.6 $\mathrm{Pg\,a^{-1}}$ for the global net uptake of carbon by epiphytic crusts (Table A7).

The total value of ~3.6 Pg a^{-1} estimated for the global net uptake of carbon by microbiotic crusts corresponds to ~6% of the estimated global net carbon uptake by terrestrial vegetation (net primary production, NPP: ~60 Pg a^{-1}, Running et al., 2004). To put this flux into perspective: it is of the same magnitude as the global annual carbon turnover due to biomass burning, which has been estimated at 3.6 Pg a^{-1} (Andreae and Merlet, 2001).

The reported values of biomass in microbiotic crusts are in the range of 1–1200 g m^{-2} (dry mass) with median values of 260 g m^{-2} for soil crusts and 130 g m^{-2} for epiphytic crusts (Table A8). By multiplication of these values with the global areas of dry-lands and forests/shrubs, respectively (Tables A2 and A7) we obtain global estimates of ~17 Pg for the biomass of BSC in arid and semi-arid regions and ~6 Pg for the biomass of EPC on evergreen leaves, on branches and stems of trees, and on tropical lianas. The total of ~23 Pg estimated for the global dry biomass of microbiotic crusts corresponds to ~10 Pg of carbon (conversion factor ~2) (Whitman et al., 1998), and thus to ~2% of the estimated global mass of carbon in terrestrial vegetation (470–650 Pg) (Prentice et al., 2001).

Microbiotic crusts do not only fix carbon, but are also able to assimilate atmospheric nitrogen. The reported average fluxes of nitrogen fixation are in the range of 0.1–10 g m^{-2} a^{-1} (Table A9). With the median values of ~0.4 g m^{-2} a^{-1} for BSC and ~0.35 g m^{-2} a^{-1} for EPC (Table A9) and using the same surface area values as above, we obtain global estimates of ~30 Tg a^{-1} and ~15 Tg a^{-1} for nitrogen fixation by BSC and EPC, respectively. Thus, the total rate of nitrogen fixation by microbiotic crusts (~45 Tg a^{-1}) appears to be a major contribution to global biological nitrogen fixation, which is estimated to be about 107 Tg a^{-1} (Galloway, 2005). Note that nitrogen fixation by microbiotic crusts is likely to be important also for the sequestration of CO_2 by terrestrial plants (CO_2 fertilization), because the latter is constrained by the availability of fixed nitrogen (Reich et al., 2006).

4 Conclusions

Overall, our calculations suggest that microbiotic crusts on soil, rock, and plants are major players in the global biogeochemical cycles of carbon and nitrogen and should thus be considered in climate and Earth system models. Regional and seasonal patterns as well as long-term trends regarding their diversity, abundance and gas exchange with the atmosphere need to be better characterized for a full mechanistic and quantitative understanding of the influence of the biosphere on climate.

Appendix A

See Tables A1–A9.

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Table A1. Annual net carbon uptake fluxes (photosynthesis minus respiration) of biological soil crusts (BSC) in arid and semiarid regions, (b) BSC in other sparsely vegetated regions, and (c) biological crusts on rocks (BRC).

Carbon uptake flux ($\mathrm{g\,m^{-2}\,a^{-1}}$)	BSC components	Habitat	Location	Calculation background	Reference
(a)					
74.9	Early and later successional stage BSC (*Nostoc/ Scytonema* or *Placidium/ Collema* dominated)	1. Pinyon-juniper woodland; 2. Shrubland	1. Cold desert Canyonlands, SE Utah 2. Warm desert Jornada site, New Mexico	Mean value of balances minus respiration	(Housman et al., 2006)
49.1	Soilcrust cyanolichen (*Collema tenax*)	Pinyon-juniper woodland	Colorado Plateau, USA	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Lange et al., 1998a)
32.7	Lichen-dominated soilcrust (*Ramalina maciformis*)	Desert mesa	Highlands of the Central Negev Desert, Israel	Adopted balance	(Kappen et al., 1980)
29.9	Soilcrust lichens (*Diploschistes diacapsis*, *Psora cerebriformis*, *Squamarina lentigera*)	Pinyon-juniper woodland	Colorado Plateau, USA maximum values of net	Calculated from photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Lange et al., 1997)
28.8	Lichen-dominated soilcrust	Pinyon-juniper woodlands	Colorado Plateau, Utah	Adopted balance	(Klopatek, 1992)
24.6	Mixed crust, cyanobacteria and chlorophyta	Orinoco Llanos	Savannah, Venezuela maximum values of net	Calculated from photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(San José and Bravo, 1991)
24.5	Lichen of BSC (*Teloschistes capensis*)	Namib lichen fields	Namib desert, Namibia	Mean value of balances	(Lange et al., 2006)
21.0	BSC dominated by cyanolichen (*Gloeoheppia turgida*)	Slopes of the Dead Sea	Judean Desert, Israel maximum values of net	Calculated from photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Lange et al., 1993)
17.0	Lichen-dominated soilcrust	Blackbrush community	Colorado Plateau, Arizona	Adopted balance	(Klopatek, 1992)
16.0	Soilcrust lichens (*Acarospora schleicheri*, *Caloplaca volkii*, *Lecidella crystallina*)	Namib lichen fields	Namib desert, Namibia	Adopted balance	(Lange et al., 1994b)
15.4	Hypolithic community dominated by cyanobacteria	Desert pavement	Joshua Tree National Park, California	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Schlesinger et al., 2003)
14.0	Poikilohydric moss carpet (*Tortula ruralis*)	Calcareous semiarid grassland	Sandy grassland, *Festucetum vaginatae danubiale*, Hungary	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Juhász et al., 2002)
13.0	BSC, lichen dominated (*Peltula richardsii*, *P. patellata*, *Placidium squamulosum*, *Psora decipiens*)	Floodplains	Sonoran Desert, Baja California	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	Büdel and Lange, unpublished
10.5	Mixed BSC with cyanobacteria, algae, mosses, and lichens	Pinyon-juniper woodland	Canyonlands National Park, Utah	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Philips and Belnap, 1998)
7.8	Cyanobacteria-dominated BSC (*Microcoleus*- and *Scytonema*-dominated)	Seasonally inundated system of pans and dunes	Western Mojave Desert	Mean value of balances minus respiration	(Brostoff et al., 2005)
6.6	Soilcrust lichens (*Squamarina* cf. *crassa*, *Diploschistes steppicus*)	Central Negev	Negev Desert, Israel	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Lange et al., 1970)
5.8	Cyanobacteria-dominated BSC (*Microcoleus* sp.)	Nizzana Dunes	Negev Desert, Israel	Calculated from maximum values of net photosynthesis $(\mathrm{NP}_{max})^{\alpha}$	(Lange et al., 1992)
1.1	Cyanobacteria-dominated BSC (*Microcoleus vaginatus*, *Nostoc* sp., *Scytonema* sp.)	Pinyon-juniper woodland	Colorado Plateau, southeastern Utah	Mean value of balances	(Garcia-Pichel and Belnap, 1996)
0.8	Cyanobacteria-dominated soilcrust (*Scytonema* sp., *Microcoleus* sp.)	Blackbrush community	Kaiparowits Basin, southern Utah	Mean value of balances	(Jeffries et al., 1993)
16.0 (median), 20.7 (arithmetic mean), 17.8 (standard deviation)					

Table A1. Continued.

Carbon uptake flux ($g\,m^{-2}\,a^{-1}$)	BSC components	Habitat	Location	Calculation background	Reference
(b)					
80.7	BSC dominated by green algae (*Klebsormidium* spp.)	Forest clear cut area	Summer green decidous forest zone, Czech Republic	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	Büdel and Lukesová, unpublished
29.9	Soilcrust chlorolichens (*Diploschistes muscorum, Squamarina lentigera, Fulgensia fulgens*)	Xerothermic steppe formation	Summer green decidous forest zone, Germany	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Lange, 2000a)
28.2 (*Squamarina lentigera*)	Chlorolichen	Xerothermic steppe formation forest zone, Germany	Summer green decidous	Adopted balance	(Lange and Green, 2004)
25.8	Cyanolichen (*Collema cristatum*)	Xerothermic steppe formation	Summer green decidous forest zone, Germany	Adopted balance	(Lange, 2000b)
20.4	Lichen community in dry dwarf shrub heath	Upland tundra	Foothills of the Brooks Range, Alaska	Adopted balance	(Lange et al., 1998b)
15.7	Lichen heath	Upland tundra	Foothills of the Brooks Range, Alaska	Adopted balance	(Lange et al., 1998b)
9.6	Lichen community in Dryas heath	Upland tundra	Foothills of the Brooks Range, Alaska	Adopted balance	(Lange et al., 1998b)
4.7	Lichen community in moist dwarf shrub heath	Upland tundra	Foothills of the Brooks Range, Alaska	Adopted balance	(Lange et al., 1998b)
23.1 (median), 26.9 (arithmetic mean), 23.5 (standard deviation)					
(c)					
21.7	Chlorolichen (*Lecanora muralis*)	Sandstone wall	Spessart midlands, Germany	Adopted balance	(Lange, 2003)
20.4	Epi- and endolithic lichens	Sandstones	Mount Zebra National Park, Cape Province and Savannah, Mutamba, northern Transvaal	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Wessels and Kappen, 1993)
16.8	Cyanobacterial mat 2. Limestone rock outcrop, 3. vertical loamy surface	1. epilithic on granite rock,	1. Inselberg, Ivory coast, 2. Paraguana Peninsula, Venezuela, 3. Northern Coastal Range, Venezuela	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Lüttge et al., 1995)
15.8	Endolithic lichens (*Hymenelia prevostii, H. coerulea*)	Endolithic habitat	Calcareous rock outcrops, Untersberg, northern Alps	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Weber et al., 2007)
12.7	Endolithic lichens (*Lecidea aff. sarcogynoides, Sarcogyne cf. austroafricana, Lecidea confluenta, Lithoglypha aggregata*)	Endolithic habitat	1. Sandstone inselberg on Mutamba Ranch, South Africa; 2. Golden Gate Highlands National Park, South Africa	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Winkler and Kappen, 1997)
8.7	Epi- and endolithic lichens	Limestone	Karst Plateau, Trieste, Italy	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Tretiach and Geletti, 1997)
8.6	Cyanobacterial mat	1. epilithic on granite rock, 2. Limestone rock outcrop, 3. vertical loamy surface	1. Inselberg, Ivory coast, 2. Paraguana Peninsula, Venezuela, 3. Northern Coastal Range, Venezuela	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Lüttge et al., 1995)
8.0	Endolithic cyanobacteria	Cryptoendolithic habitat	Sandstone plateau along Brakrivier, Northern Transvaal, South Africa	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Weber, 1994)
7.4	Cyanobacteria/ cyanolichen crusts	Inselberg	Dry savanna, South Africa	Adopted balance	(Büdel, 1999)
7.0	Epilithic lichen (*Acarospora* sp.)	Sandstones	Mount Zebra National Park, South Africa	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Wessels and Kappen, 1993)
6.9	Epi- and endolithic lichens	Epilithic and endolithic on limestone; *Caloplaca ehrenbergii* on chert	Central Negev Desert, Israel	(Lange et al., 1970) maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	
3.9	Cryptoendolithic cyanobacteria together with green algae	Temperate zone sandstone	Colorado Plateau, Arizona	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Bell and Sommerfeld, 1987)
3.5	Endolithic lichen (Verrucaria baldensis)	Limestone	Karst Plateau, Trieste, Italy	Calculated from maximum values of net photosynthesis $(NP_{max})^{\alpha)}$	(Tretiach and Geletti, 1997)
3.3	Cyanobacteria/ cyanolichen crusts	Inselberg	Humid savanna, Venezuela	Adopted balance	(Büdel, 1999)
2.3	Cyanobacteria/ cyanolichen crusts	Inselberg	Thorn bush savannah, South Africa	Adopted balance	(Büdel, 1999)
0.6	Lichen-dominated endolithic community with green algae and cyanobacteria	Cryptoendolithic habitat	Beacon sandstone of the Ross Desert, Antarctica	Adopted balance	(Friedmann et al., 1993)
7.7 (median), 9.2 (arithmetic mean), 6.5 (standard deviation)					

$^{\alpha)}$ NP_{max} values were scaled to estimated average ambient conditions.

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Table A2. Global surface area of terrestrial arid and semiarid regions (dry-lands).

Area (10^{13} m^2)	References
7.8	(Watson et al., 2000)
6.8	(Asner et al., 2003)
6.6	(Ramankutty and Foley, 1999)
6.5	(Whittaker and Likens, 1973)
6.4	(Garcia-Pichel et al., 2003)
6.0	(Kucharik et al., 2000)
5.5	(Goldewijk, 2001)
5.0	(Ajtay et al., 1979)
5.0	(Lawrence and Chase, 2007)
6.4 (median), 6.2 (arithmetic mean), 0.9 (standard deviation)	

Table A3. Annual net carbon uptake flux (photosynthesis minus respiration) of epiphytic and epiphyllic crusts (EPC).

Carbon uptake flux ($g\,m^{-2}\,a^{-1}$)	EPC components	Habitat	Location	Calculation background	Reference
167.7	Homoiomerous cyanolichen (*Leptogium cyanescens*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2000)
116.3	Homoiomerous cyanolichen (*Leptogium phyllocarpum*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2000)
86.0	Epiphytic *Lobariaceae* (*Sticta weigelii*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2004)
78.9	Cyanobacterial basidiolichen (*Dictyonema glabratum*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 1994a)
74.2	Epiphytic *Lobariaceae* (*Sticta sublimbata*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2004)
60.2	Epiphytic *Lobariaceae* (*Sticta tomentosa*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Zotz et al., 1998)
29.5	Epiphytic *Lobariaceae* (*Pseudocyphellaria intricata*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2004)
26.8	Homoiomerous cyanolichen (*Leptogium azureum*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2000)
25.4	Epiphytic *Lobariaceae* (*Pseudocyphellaria aurata*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Adopted balance	(Lange et al., 2004)
9.3	Corticolous lichen (*Coenogonium linkii*)	Tropical evergreen lowland rainforest	Les Nouragues National Park, French Guiana	Calculated from maximum values of net photosynthesis (NP_{max})$^{\alpha)}$	(Lakatos et al., 2006)
5.6	Epiphytic *Lobariaceae* (*Lobaria crenulata*)	Lower montane rainforest	Cordillera Central, Republic of Panama	Calculated from maximum values of net photosynthesis (NP_{max})$^{\alpha)}$	(Lange et al., 2004)
2.7	Corticolous lichen (*Cryptothecia rubrocincta*)	Tropical evergreen lowland rainforest	Les Nouragues National Park, French Guiana	Calculated from maximum values of net photosynthesis (NP_{max})$^{\alpha)}$	(Lakatos et al., 2006)
1.9	Corticolous lichen (*Thelotrema alboolivaceum*)	Tropical evergreen lowland rainforest	Les Nouragues National Park, French Guiana	Calculated from maximum values of net photosynthesis (NP_{max})$^{\alpha)}$	(Lakatos et al., 2006)
1.1	Corticolous lichen (*Phyllopsora corallina*)	Tropical evergreen lowland rainforest	Les Nouragues National Park, French Guiana	Calculated from maximum values of net photosynthesis (NP_{max})$^{\alpha)}$	(Lakatos et al., 2006)
(37–64)	Epiphytic bryophytes lower montane wet forest	Tropical	Costa Rica	Adopted balance	(Clark et al., 1998)
28.2 (median), 49.0 (arithmetic mean), 50.5 (standard deviation)					

$^{\alpha)}$ NP_{max} values were scaled to estimated average ambient conditions.

Table A4. Global tropical forest area.

Forest area (10^{13} m^2)	References
1.9	(Kucharik et al., 2000)
1.8	(Watson et al., 2000)
1.7	(Matthews, 1983)
1.7	(Whittaker and Likens, 1973)
1.7	(Ramankutty and Foley, 1999)
1.6	(Prigent et al., 2001)
1.5	(Matthews, 1983)
1.5	(Ajtay et al., 1979)
1.4	(Lawrence and Chase, 2007)
1.3	(Matthews, 1983)
1.7 (median), 1.6 (arithmetic mean), 0.2 (standard deviation)	

Table A5. Plant surface area of (a) leaves of tropical evergreen trees (leaf area index, LAI), (b) tropical lianas (LAI), (c) leaves of evergreen trees and shrubs (LAI; temperate and boreal), and (d) stems and branches of trees and shrubs (wood area index, WAI; stem area index, SAI).

Area index ($m^2\ m^{-2}$)	Forest type	Location	References
(a)			
12.3	Tropical lowland rainforest	Thailand	(Arora and Boer, 2005)
8.0	Tropical rainforest	Global average	(Whittaker and Likens, 1973)
7.4	Evergreen tropical forest	Thailand	(Putz, 1983)
7.3	Subtropical wet forest	Puerto Rico	(Weaver et al., 1986)
7.3	Tropical lowland rainforest	Malaysia	(Putz, 1983)
6.0 (up to 13)	Tropical upland wet forest	Costa Rica	(Clark et al., 2008)
5.5	Rubber tree forest	Maharastra, India	(Devakumar et al., 1999)
5.2	Tropical rainforest	Rio Negro Basin, Venezuela	(Putz, 1983)
5.0	Lower montane rainforest	Puerto Rico	(Weaver and Murphy, 1990)
4.8	Tropical evergreen broadleaf forest	Global average	(Scurlock et al., 2001)
4.7	Tropical deciduous forest	Mexico	(Arora and Boer, 2005)
4.0	Broadleaf forests	Amazon	(Buermann et al., 2002)
3.3	Lower montane rainforest	Puerto Rico	(Weaver and Murphy, 1990)
2.0	Lower montane rainforest	Puerto Rico	(Weaver et al., 1986)
(5–8)	Tropical forest	Amazon	(Arora and Boer, 2005)
(6–7)	Subtropical wet forest	Puerto Rico	(Weaver and Murphy, 1990)
(3–5)	Lower montane rainforest	Puerto Rico	(Weaver and Murphy, 1990)
(3–3.5)	Lower montane rainforest	Puerto Rico	(Weaver and Murphy, 1990)
5.4 (median), 5.9 (arithmetic mean), 2.5 (standard deviation)			

Table A5. Continued.

Area index ($m^2\,m^{-2}$)	Forest type	Location	References
(b)			
3.3	Lianas in tropical forest	Brazilian Amazon	(Gerwing and Farias, 2000)
3.3	Lianas in tropical forest	Brazilian Amazon	(Gerwing and Vidal, 2002)
1.7	Lianas and vines in tropical deciduous forest	Mexico	(Castellanos et al., 1992)
1.2	Lianas in evergreen tropical rain forest	Rio Negro Basin, Venezuela	(Putz, 1983)
0.7	Lianas in tropical upland wet forest	Costa Rica	(Clark et al., 2008)
(2–7)	Lianas in lowland tropical rain forest	Gabon	(Kazda and Salzer, 2000)
1.7 (median), 2.0 (arithmetic mean), 1.2 (standard deviation)			
(c)			
5.3	Mediterranean oak forest	Spain	(Sala et al., 1994)
4.6	Mediterranean oak forest	Spain	(Sala et al., 1994)
4.3	Mediterranean evergreen maquis	Portugal	(Caldwell et al., 1986)
2.9	Coastal oak forest	Bulgaria	(Wiman and Gaydarova, 2008)
2.5	Mediterranean evergreen maquis	Italy	(Gratani and Varone, 2007)
2.5	Mediterranean evergreen maquis	Sardinia, Italy	(Rossi et al., 2001)
(1.4–3.2)	Coastal oak forest	Bulgaria	(Gaydarova, 2003)
3.6 (median), 3.7 (arithmetic mean), 1.2 (standard deviation)			
(d)			
1.9[a]	Douglas fir forest	Oregon coast range, USA	(Weiskittel and Maguire, 2006)
1.3[a]	Mixed forest	Belgium	(Vincke et al., 2005)
1.3[b]	Mediterranean oak forest	Spain	(Sala et al., 1994)
0.7[a]	Tropical dry forest	Mexico, Costa Rica, Brazil	(Sánchez-Azofeifa et al., in press)
0.5[a]	Tropical dry forest	Mexico, Costa Rica, Brazil	(Sánchez-Azofeifa et al., in press)
(2.0–2.6)[c]	Rainforests	Japan and Southeast Asia	(Yoneda, 1993)
(0.4–2.5)[a]	Mixed forest	Alsace, France	(Breda, 2003)
(0.5–1.9)[c]	Norway spruce forest	Germany	(Falge et al., 1997)
(0.3–1.5)[a]	Mixed forest	France	(Dufrêne and Bréda, 1995)
1.3 (median), 1.1 (arithmetic mean), 0.6 (standard deviation)			

[a] WAI

[b] SAI, but main trunks excluded

[c] SAI

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Table A6. Plant surface coverage by EPC on (a) leaves, (b) needles, and (c) stems and branches.

Coverage (%)	EPC components	Location, host plant	Reference
(a)			
~100	Liverworts	Humid tropical forests	(Berrie and Eze, 1975)
> 90	Bryophytes	Tropical lowland rainforest in Costa Rica	(Fürnkranz et al., 2008)
(50–100)	Lichens	Tropical rainforests	(Anthony et al., 2002)
(25–31)	Epiphyll cover	Coffee plants, semi-hot humid climate	(Roskoski, 1981)
(20–30) (up to 70)	Bryophytes	Rainforest in Costa Rica, understory plants	(Freiberg, 1998, 1999)
(22–35)	Lichens	Moist forests of Panama	(Coley et al., 1993)
(2–20)	Liverworts	Moist forests of Panama	(Coley et al., 1993)
(2–10)	Cyanobacteria	Rainforest in Costa Rica, understory plants	(Freiberg, 1998, 1999)
(b)			
58	Alectorioid lichens	Old-growth Pseudotsuga-Tsuga forests, Pacific Northwest, USA	(McCune et al., 1997)
55	Epiphyllic lichen (*Hypogymnia physodes*)	Conifers, temperate European sites	(Søchting, 1997)
27	Bryophytes	Old-growth Pseudotsuga-Tsuga forests, Pacific Northwest, USA	(McCune et al., 1997)
25	Various lichens	Old-growth Pseudotsuga-Tsuga forests, Pacific Northwest, USA	(McCune et al., 1997)
17	Cyanolichens	Old-growth Pseudotsuga-Tsuga forests, Pacific Northwest, USA	(McCune et al., 1997)
8	Actinomycetes, fungi, and algae	Douglas fir, Oregon, USA	(Bernstein and Carroll, 1977)
7	Microepiphyte cover	Douglas fir, Oregon, USA	(Pike et al., 1977)
5	Actinomycetes, fungi, and algae	Douglas fir, Oregon, USA	(Carroll, 1979)
(45–80)	Green algae, fungi, and bacteria	Spruce trees, Germany	(Peveling et al., 1992)
(32–77)	Epiphytes (chlorolichens, cyanolichens, and bryophytes)	Sitka spruce, California, USA	(Ellyson and Sillett, 2003)
(c)			
~100	Crustose lichens	Lowland forest, Panama	(Zotz, 1999)
38	Crustose lichens	Lowland rainforest, Costa Rica	(Forman, 1975)
(40–100)	Bryophytes (2–14 cm in thickness)	Montane rainforests, Ecuador	(Freiberg and Freiberg, 2000)
(3–83) (most between 20–50)	Corticolous and crustose microlichens	Atlantic rainforest, Brazil	(Cáceres et al., 2007)
(40–80)	Foliose and crustose lichens	Forest in Norway	(Solhaug et al., 1995)
(25–60) (up to 80)	Mosses, liverworts, cyanolichens and other lichens	Douglas fir, Oregon, USA	(Sherwood and Carroll, 1974; Sillett, 1995; Sillett and Rambo, 2000)
(2–50)	Bryophytes (2–14 cm in thickness)	Lowland rainforests, Ecuador	(Freiberg and Freiberg, 2000)

Table A7. Annual net carbon uptake by EPC in forest and shrub areas.

Substrate	Area index[a] (m^2 m^{-2})	Forest/ shrub area (10^{13} m^2)	Plant surface area (10^{13} m^2)	EPC coverage[d] (%)	EPC covered surface area (10^{13} m^2)	Annual net carbon uptake[e] (Pg a^{-1})
Leaves of tropical evergreen trees	5.4	1.7[b]	9.2	50	4.7	1.3
Tropical lianas	1.7	1.7[b]	2.9	50	1.6	0.4
Leaves of evergreen trees and shrubs; temperate and boreal	3.6	1.0[c]	3.6	30	1.0	0.3
Stems and branches of trees and shrubs	1.3	4.4[c]	5.7	35	2.3	0.6
Total		4.4[c]			9.6	2.6

[a] see Table A5;
[b] see Table A4;
[c] from "Community Land Model" (CLM 3.0) (Lawrence and Chase, 2007);
[d] estimated from values given in Table A6;
[e] calculated assuming a median carbon net fixation rate of 28 g m^{-2} (Table A3).

Table A8. Estimated global biomass (dry weight) of (a) BSC, (b) BRC, (c, d) EPC. Values in (a–c) in g m^{-2} of ground surface area, (d) in g m^{-2} of thallus or branch surface area.

Biomass (g m^{-2})	Component	Location	Reference
(a)			
1187	Soilcrust cyanolichen (*Collema tenax*)	Pinyon-juniper woodland, Colorado Plateau, USA	(Lange et al., 1998a)
684	Chlorolichen (*Squamarina lentigera*)	Xerothermic steppe formation, Germany	(Lange and Green, 2004)
447	Lichen of BSC (*Teloschistes capensis*)	Namib Desert, Namibia	(Lange et al., 2006)
306	Cyanolichen (*Collema cristatum*)	Xerothermic steppe formation, Germany	(Lange, 2000b)
258	Lichen community in dry dwarf shrub heath	Upland Tundra, Brooks Range, Alaska	(Lange et al., 1998b)
219	Lichen heath	Upland Tundra, Brooks Range, Alaska	(Lange et al., 1998b)
155	Lichen community in Dryas heath	Upland Tundra, Brooks Range, Alaska	(Lange et al., 1998b)
65	Lichen-dominated soilcrust (*Ramalina maciformis*)	Desert mesa, Central Negev Desert, Israel	(Kappen et al., 1980)
57	Lichen community in moist dwarf shrub heath	Upland Tundra, Brooks Range, Alaska	(Lange et al., 1998b)
(1–16)	Edaphic cyanobacteria	Various locations on Earth	(Garcia-Pichel et al., 2003)
(1–12)	Soil crust cyanobacteria	Various locations, Russia	(Pankratova, 2006)
258 (median), 375.3 (arithmetic mean), 362.0 (standard deviation)			
(b)			
594	Epilithic chlorolichen (*Aspicilia radiosa*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
243	Cyanobacterial biofilm	Inselberg, tropical rainforest, French Guiana	(Dojani et al., 2007)
336	Endolithic cyanobacteria community	Mt. Falconer, Antarctica	(Büdel et al., 2008)
117	Endolithic chlorolichen (*Verrucaria sp.*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
50	Nearly endolithic chloroplichen (*Acrocordia conidea*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
50	Endolithic chlorolichen (*Verrucaria marmorea*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
30	Nearly endolithic chlorolichen (*Petractis clausa*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
30	Endolithic chlorolichen (*Rinodina immersa*)	Limestone karst plateau, Trieste, Italy	(Tretiach, 1995)
(38–185)	Endolithic microbial communities in sandstone and granite	Mojave Desert, California; Sonoran Desert, Mexico; Negev Desert, Israel	(Friedmann, 1980)
(32–177)	Endolithic microbial communities	Beacon sandstone, Dry Valley, Antarctica	(Friedmann, 1980)
(4–107)	Endolithic cyanobacteria community	Tshipise sandstone formation, South Africa	(Büdel et al., 2004)
(2–73)	Endo- and epilithic algae, cyanonacteria, and lichens	Niagara Escarpment, Ontario, Canada	(Matthes-Sears et al., 1997)
84 (median), 181.3 (arithmetic mean), 200.9 (standard deviation)			

Table A8. Continued.

Biomass (g m^{-2})	Component	Location	Reference
(c)			
1013	Epiphytic bryophytes (*Frullania atrata*, *Phyllogonium fulgens*) and epiphyllous algae (*Trentepohlia*)	Tropical rainforest (at greater depth within cloud forest canopy), Guadeloupe, French West Indies	(Coxson et al., 1992)
422	Epiphytic non-crustose lichens and bryophytes	Mt. Baker, Washington, USA	(Rhoades, 1981)
332	Epiphytic lichens and bryophyts	Old-growth conifer forest, Pacific northwest, USA	(McCune et al., 1997)
221	Epiphytic bryophytes (*Frullania atrata*, *Phyllogonium fulgens*) and epiphyllous algae (*Trentepohlia*)	Tropical rainforest (upper 1.5 m of cloud forest canopy), Guadeloupe, French West Indies	(Coxson et al., 1992)
200	Epiphytic mosses (mainly *Hypnum andoi*)	Vosges Mountains, France	(Frahm, 2008)
155	Epiphytic cyanolichens, alectorioid and other lichens, and bryophytes	Pseudotsuga, Thuja and Tsuga stands in Oregon and Washington, USA	(McCune, 1993)
125	Epiphytic cyanolichens, alectorioid and other lichens, and bryophytes	Pseudotsuga, Thuja and Tsuga stands in Oregon and Washington, USA	(McCune, 1994)
104	Epiphytic lichens (dominated by *Pseudevernia* spp.)	Fir plantation, Massif du Pilat, Loire, France	(André et al., 1975)
84	Epiphytic lichens (*Lobaria*, *Usnea*, *Hypogymnia*, *Alectoria*, and *Parmelia* spp.)	Conifer, oak and northern hardwood forests, Canada and USA	(Pike, 1978)
55	Cyanolichen (*Lobaria oregana*)	Douglas fir and western hemlock dominated forest, Pacific Northwest, USA	(Brown and Dalton, 2002)
41	Epiphytic lichens (*Alectoria* spp., *Bryoria* spp., and foliose lichens)	Entire needle trees, British Columbia, Canada	(Campbell and Coxson, 2001)
1	Epiphytic noncrustose cyanolichens	Very moist submontane forest, (2700 m a.s.l.), Colombia	(Forman, 1975)
(63–350)	Non-crustose lichens and bryophytes	Varies forests in USA and Canada	(Rhoades, 1981)
(90–260)	Epiphytic lichens (*Alectoria* spp., *Bryoria* spp., *Usnea* spp., fruticose lichens, and cyanolichens) and mosses	Old-growth Douglas fir forest in Oregon, USA	(Sillett and Rambo, 2000)
(108–133)	Canopy lichen community	Wet-temperate rainforest, British Columbia, Canada	(Benson and Coxson, 2002)
(39–50)	Lichen spp.	Douglas fir forest, Oregon, USA	(Becker, 1980)
(<1)	Epiphytic cyanolichens	Gray beech forests, North Carolina, USA	(Becker, 1980)
140 (median), 204.5 (arithmetic mean), 278.7 (standard deviation)			

Table A8. Continued.

Biomass (g m^{-2})	Component	Location	Reference
(d)			
192$^{a)}$	Lichens (*Sticta* sp.)	Rainforest, Colombia	(Forman, 1975)
167$^{a)}$	Lichens with green algae	Rainforest, Colombia	(Forman, 1975)
162$^{a)}$	Epiphytic cyanolichens	Appalachian Mountains, North Carolina, USA	(Becker, 1980)
153$^{a)}$	Lichens with non-heterocystic cyanobacteria	Rainforest, Colombia	(Forman, 1975)
151$^{a)}$	Homoiomerous cyanolichen (*Leptogium phyllocarpum*)	Lower montane rainforest, Cordillera Central, Republic of Panama	(Lange et al., 2000)
136$^{a)}$	Lichens (*Leptogium* sp.)	Rainforest, Colombia	(Forman, 1975)
134$^{a)}$	Epiphytic *Lobariaceae* (*Sticta tomentosa*)	Lower montane rainforest, Cordillera Central, Republic of Panama	(Zotz et al., 1998)
129$^{a)}$	Homoiomerous cyanolichen (*Leptogium cyanescens*)	Lower montane rainforest, Cordillera Central, Republic of Panama	(Lange et al., 2000)
105$^{a)}$	Homoiomerous cyanolichen (*Leptogium azureum*)	Lower montane rainforest, Cordillera Central, Republic of Panama	(Lange et al., 2000)
70$^{a)}$	Cyanobacterial basidiolichen (*Dictyonema glabratum*)	Lower montane rainforest, Cordillera Central, Republic of Panama	(Lange et al., 1994a)
53$^{a)}$	Corticolous lichen (*Coenogonium linkii*)	Tropical evergreen lowland forest, Les Nouragues National Park, French Guiana	(Lakatos et al., 2006)
(10–720)$^{b)}$	Epiphytic lichens and bryophytes	Montane and lowland rainforests, Ecuador	(Freiberg and Freiberg, 2000)
136 (median), 132 (arithmetic mean), 41.7 (standard deviation)			

a) per m^2 of thallus surface area;
b) per m^2 of branch surface area.

Table A9. Estimated annual fluxes of nitrogen fixation by (a) BSC and (b) EPC.

Nitrogen fixation flux $(\mathrm{g\,m^{-2}\,a^{-1}})$	Crust components	Location	Reference
(a)			
5.7	BSC, cyanobacteria	Western Kalahari, Botswana	(Skarpe and Henriksson, 1987)
1.3	BSC, undisturbed	Cold desert, Utah, USA	(Belnap, 2002)
$1.0^{a)}$	BSC, cyanobacteria	Semiarid grassland, Arizona, USA	(Mayland et al., 1966)
0.6	BSC, cyanobacteria	Savanna, Nigeria	(Isichei, 1980)
0.4	BSC, cyanobacterium	Tropical volcano, Guadeloupe	(Sheridan, 1991b)
0.4	BSC	Lake Michigan sand dunes, USA	(Thiet et al., 2009)
0.2	Cyanobacteria on soil	Signy Island, South Orkney Islands	(Horne, 1972)
0.14	BSC, disturbed	Cold desert, Utah, USA	(Belnap, 2002)
0.13	BSC	Southern Utah, USA	(Veluci et al., 2006)
(0.2–37)	BSC, cyanobacteria and cyanolichens	Desert ecosystems	(Belnap et al., 2001)
(2.5–10.0)	BSC, cyanobacteria	Great Basin desert, Utah, USA	(Veluci et al., 2006)
(0.1–10.0)	BSC	Various (semi-)arid locations	(Evans and Lange, 2003)
(0.7–1.8)	BSC	Sonoran Desert, Arizona, USA	(Veluci et al., 2006)
(0.9–1.3)	BSC, undisturbed	Cold desert, Utah, USA	(Belnap, 2002)
(0.1–0.2)	Bryophyte-cyanobacteria	Antarctica	(Turetsky, 2003)
0.4 (median), 1.1 (arithmetic mean), 1.8 (standard deviation)			
(b)			
42.3	EPC, cyanobacteria (*Nostoc* and *Stigonema* spp.)	Mangrove boles and branches, Guadeloupe, French West Indies	(Sheridan, 1991a)
3.8	EPC, cyanobacteria (*Calothrix* and *Lyngbya* spp.)	*Spartina alterniflora* stems, transplanted salt marsh, North Carolina, USA	(Currin and Pearl, 1998)
2.6	EPC, cyanobacteria (*Calothrix* and *Lyngbya* spp.)	*Spartina alterniflora* stems, natural salt marsh, North Carolina, USA	(Currin and Pearl, 1998)
$0.5^{b)}$	EPC, cyanobacteria (*Calothrix* and *Anabaena* spp.)	*Spartina alterniflora* leaves and stems, salt marsh, Georgia, USA	(Hanson, 1977)
$0.2^{c)}$	EPC, cyanobacteria (*Calothrix* and *Anabaena* spp.)	*Spartina alterniflora* leaves and stems, salt marsh, Georgia, USA	(Hanson, 1977)
0.2	EPC, symbiotic cyanobacterium (*Nostoc* sp.) within feather moss (*Pleurozium schreberi*)	Boreal forests	(DeLuca et al., 2002)
0.2	Epiphytic lichens	Old-growth Douglas fir forest of Pacific Northwest, USA	(Brown and Dalton, 2002)
0.15	Epiphytic cyanolichens (*Lobaria oregana*)	Pseudotsuga, Thuja and Tsuga stands (WRCC site), Washington, USA	(Antoine, 2004)
(0–6)	EPC	Temperate and tropical regions	(Freiberg, 1998)
(0.3–1.7)	Epiphytic cyanolichens (*Lobaria oregana*)	Pseudotsuga, Thuja and Tsuga stands (HJA site), Washington, USA	(Antoine, 2004)
(0.2–0.8)	Epiphytic lichens	Rainforest in Colombia (2700 m a.s.l.)	(Forman, 1975)
(0.2–0.5)	Understory EPC, cyanobacteria	Premontane rainforest in Costa Rica	(Freiberg, 1998)
(0.1–0.5)	Epiphytic lichens	Scotland and Sweden	(Forman, 1975)
0.35 (median), 6.2 (arithmetic mean), 14.6 (standard deviation)			

[a)] maximum; [b)] average from control and experimental plot – 10 h fixation period estimate; [c)] average from control and experimental plot – 24 hour fixation period estimate.

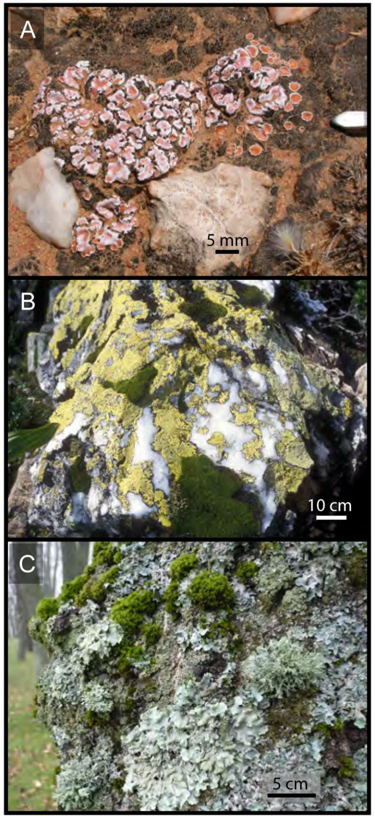

Fig. 1. Exemplary photographs of microbiotic crusts. **(A)** Biological soil crust (BSC) showing cyanobacteria and chlorolichen *Psora decipiens*, Nama Karoo semi desert, Western Cape, South Africa. **(B)** Biological rock crust (BRC) showing chlorolichen (*Rhizocarpon geographicum* aggr.), Sadnig, Eastern Alps, Austria. **(C)** Epiphytic crust (EPC) showing lichen and bryophytes on *Acer pseudoplatanus* tree in a city park, Trier, Germany.

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