Enhanced interplanetary panspermia in the TRAPPIST-1 system

Manasvi Lingam[a,b,1] **and Abraham Loeb**[b]

[a]John A. Paulson School of Engineering and Applied Sciences, Harvard University, Cambridge, MA 02138; and [b]Institute for Theory and Computation, Harvard–Smithsonian Center for Astrophysics, Cambridge, MA 02138

Edited by Neta A. Bahcall, Princeton University, Princeton, NJ, and approved May 10, 2017 (received for review March 1, 2017)

We present a simple model for estimating the probability of interplanetary panspermia in the recently discovered system of seven planets orbiting the ultracool dwarf star TRAPPIST-1 and find that panspermia is potentially orders of magnitude more likely to occur in the TRAPPIST-1 system compared with the Earth-to-Mars case. As a consequence, we argue that the probability of abiogenesis is enhanced on the TRAPPIST-1 planets compared with the solar system. By adopting models from theoretical ecology, we show that the number of species transferred and the number of life-bearing planets are also likely to be higher because of the increased rates of immigration. We propose observational metrics for evaluating whether life was initiated by panspermia on multiple planets in the TRAPPIST-1 system. These results are also applicable to habitable exoplanets and exomoons in other planetary systems.

exoplanets | panspermia | origin of life | astrobiology

The field of exoplanetary research has witnessed remarkable advances in the past two decades, with the total number of discovered exoplanets now numbering in the thousands (1). This progress has been accompanied by a better understanding of the factors that make a planet habitable (i.e., capable of supporting life) (2). It is now well-known that there exist $\sim 10^{10}$ habitable planets in the Milky Way, many of which orbit M dwarfs (3). Planets in the habitable zone (HZ)—the region theoretically capable of supporting liquid water—of M dwarfs have been extensively studied, because they are comparatively easier to detect and analyze (4).

The search for exoplanets around nearby low-mass stars has witnessed two remarkable advances over the past year, namely (*i*) the discovery of Proxima Centauri b, the nearest exoplanet to the solar system (5), and (*ii*) the discovery of seven planets transiting the ultracool dwarf star TRAPPIST-1 (6). The latter is all of the more remarkable, because three of seven planets reside within the HZ; also, each of them has a mass and a radius that are nearly equal to those of the Earth (7). Hence, the TRAPPIST-1 transiting system represents a unique opportunity for carrying out additional observations to determine whether these planets possess atmospheres and perhaps, even biosignatures (8).

If conditions favorable for the origin of life (abiogenesis) exist on one of the TRAPPIST-1 planets, this possibility raises an immediate question with profound consequences: could life spread from one planet to another (panspermia) through the transfer of rocky material? Panspermia has been widely investigated in our own solar system as a potential mechanism for transporting life to or from the Earth (9–13). The planets in the HZ of the TRAPPIST-1 system are separated only by ~ 0.01 a.u., tens of times less than the distance between Earth and Mars. Thus, one would be inclined to hypothesize that panspermia would be enhanced in this system.

Here, we explore this possibility by proposing a simple quantitative model for panspermia within the TRAPPIST-1 system. We show that the much higher probability of panspermia leads to a correspondingly significant increase in the probability of abiogenesis. We also draw on models from theoretical ecology to support our findings and extend our analysis to other planetary systems.

Lithopanspermia—A Simple Model

Let us suppose that the total number of rocks ejected from the host planet (Planet X) during a single event is N_x, and assume that the rocks are emitted isotropically. The number of rocks that successfully impact the target planet (Planet Y) at an average distance of D_{xy} from Planet X is

$$N_y = N_x \cdot \frac{\sigma_y}{4\pi D_{xy}^2}, \qquad [1]$$

where σ_y is the effective cross-sectional area of Planet Y. The second factor on the right-hand side (RHS) represents the fraction of rocks captured per event.

Naively speaking, we may expect $\sigma_y = \pi R_y^2$, where R_y is the radius of Planet Y. However, this estimate, which is strictly valid only for direct impact, would be many orders of magnitude smaller than the actual value in most cases. Instead, we use a simple model, wherein the rocks are captured by Planet Y provided that they fall within its gravitational sphere of influence (14). In this model,

$$\sigma_y = \eta_{xy}\, \pi\, a_y^2 \left(\frac{M_y}{2M_\star}\right)^{\frac{2}{3}}, \qquad [2]$$

where a_y and M_y are the semimajor axis and mass of Planet Y, respectively, and $M_\star$ is the mass of the host star; η_{xy} is an amplification factor introduced to account for the effects of gravitational focusing, secular resonances, etc. Combining Eqs. **1** and **2**, we arrive at

$$P_{xy} = \frac{N_y}{N_x} = 0.16\, \eta_{xy} \left(\frac{a_y}{D_{xy}}\right)^2 \left(\frac{M_y}{M_\star}\right)^{\frac{2}{3}} \qquad [3]$$

as the cumulative fraction of rocks ejected from Planet X that will impact Planet Y. We also introduce the average transit time τ_{xy} that is given by

$$\tau_{xy} = \frac{D_{xy}}{\langle v \rangle}, \qquad [4]$$

Significance

The search for extraterrestrial life is one of the most exciting frontiers in present-day astronomy. Recently, the TRAPPIST-1 star was discovered to host seven rocky planets with masses and radii similar to those of the Earth, of which at least three of them may be capable of supporting life. Our paper addresses the possibility that life on one of these planets can spread to others through the transfer of rocky material. We conclude that this process has a high probability of being operational, implying that this planetary system may possess multiple life-bearing planets. Thus, our work has profound theoretical and observational consequences for future studies of the TRAPPIST-1 system and the likelihood of life in our galaxy.

Author contributions: M.L. and A.L. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. Email: manasvi@seas.harvard.edu.

where $\langle v \rangle$ is the average velocity of the ejected rocks.

We can now attempt to calibrate this model in the solar system by choosing X and Y to be Earth and Mars, respectively. Substituting the appropriate values, we obtain $P_{EM} \sim 0.75\,\eta_{EM} \times 10^{-5}$. On comparison with the older simulations carried out in refs. 10, 15, and 16, we find that $\eta_{EM} \sim 20 - 200$. Similarly, if we use the recent value for P_{EM} from table 4 of ref. 13, we obtain $\eta_{EM} \approx 270$. Next, we consider the TRAPPIST-1 system with X and Y being TRAPPIST-1e and TRAPPIST-1f, respectively. On substituting the appropriate parameters (7), we find

$$P_{ef} \approx 0.04 \left(\frac{\eta_{ef}}{\eta_{EM}} \right), \qquad [5]$$

which implies that a nontrivial percentage of the rocks ejected from TRAPPIST-1e during each impact event will land on TRAPPIST-1f. As a result, the fraction of rocks that are transferred between planets would be comparable with (although smaller than) the fraction of rocks that fall back on the surface of the originating planet. [Gravitational perturbations by the densely packed planets could also disperse the "cloud" of rocks out of the planetary system (caused by unstable orbits).] This conclusion is fully consistent with the previous numerical simulations undertaken by ref. 17. Thus, the TRAPPIST-1 system is expected to be more efficient than the Earth-to-Mars case in facilitating panspermia.

It should be noted that P_{xy} only quantifies the fraction of rocks that impact the target planet and does not quantify the total number. The latter is dependent on N_x, which is governed by the frequency and magnitude of impacts (10, 18); the crater impact rate itself is regulated by the properties of the planetary system under consideration (19). Hence, we shall not attempt to quantify N_x (or N_y) for the TRAPPIST-1 system, because there are too many unknown factors involved. We reiterate that P_{xy} is the fraction of rocks transferred per event, and to obtain the total estimate, a knowledge of the total number of impacts over the planetary system's lifetime is required, which cannot be quantified at this stage.

Moreover, panspermia does not merely depend on the fraction of rocks transferred but also depends on other factors. Many of them have to do with the survival of microorganisms during the processes of ejection from X, transit from X to Y, and reentry on Y (20). Because of the biological characteristics of the organisms in question, one cannot quantify these probabilities; even for Earth-based microbes, there exist uncertainties (21). However, if we assume that $\bar{v}$ is the same for Earth and most of the TRAPPIST-1 planets, we see that the transit time in Eq. **4** among the TRAPPIST-1 habitable planets is about 100 times shorter than that of Earth to Mars. A higher value of $\bar{v}$, albeit one much lower that the escape velocity, could reduce the transit time even further (e.g., becoming four to five orders of magnitude lower than the Earth-to-Mars value). Hence, if the probability of surviving the transit is inversely proportional to τ_{xy}, the survival probabilities of microbes on the TRAPPIST-1 system could be several orders of magnitude higher.

We emphasize that the above model does not explicitly take into account the architecture of a given planetary system, thereby neglecting effects arising from gravitational focusing, resonances, eccentricity, and mutual inclination to name a few (1). We have also implicitly assumed that the planets settled into their present orbits quickly and that there exists a sufficiently high number of meteorites to cause spallation (12). Many of these aspects can only be studied through detailed numerical models, which fall outside the scope of this work. Despite these simplifications, our conclusions are in agreement with recent numerical simulations (17), which had incorporated most of the aforementioned factors.

Consequences for Abiogenesis

We now turn our attention to quantifying the implications of panspermia in promoting abiogenesis by drawing on an equation similar to that developed by Frank Drake in the context of the Search for Extraterrestrial Intelligence. The primary parameter of interest is the probability λ of life arising per unit time (22, 23). According to the Drake-type equation proposed in ref. 24, λ is computed as follows:

$$\lambda = \frac{N_b}{\langle n_0 \rangle} \cdot f_c \cdot P_a, \qquad [6]$$

where N_b is number of potential building blocks, $\langle n_0 \rangle$ is the mean number of building blocks per organism, f_c is the fractional availability of these building blocks during a given timespan, and P_a is the probability of abiogenesis per unit time and a suitable set of these building blocks. All of the factors, apart from P_a, are dependent on complex biological and planetary factors, which we shall not address here.

Instead, we mirror the approach outlined in ref. 24, where P_a can typically be enhanced via panspermia by a factor

$$P_a = P_0\, E^n, \qquad [7]$$

where n is the number of panspermia events, P_0 is the probability in the absence of panspermia (i.e., with $n = 0$), and E is the enhancement arising from each event. A few clarifications are in order: by "enhancement," we refer to the fractional increase in the number of molecular building blocks (not biological species) transferred per event. This condition is a less stringent requirement, possibly extant even in our own solar system (25), implying that this mechanism of "pseudopanspermia" has a higher chance of being effective.

At this stage, it is equally important to highlight the limitations of the above ansatz. The exponential gain represents an idealized scenario, namely the most positive outcome possible. In reality, the scaling with n would be much weaker, possibly being algebraic (or even logarithmic). In addition, the introduction of these new molecular "species" does not necessarily enhance the probability of abiogenesis, because they could have landed in a habitat on the planet that is inimical for their survival and growth. Moreover, the reaction networks (protometabolic or otherwise) contributing to abiogenesis and subsequent evolution could have been primarily engendered by the multitude of environmental planets on the planet (26) as opposed to external contributions through panspermia.

The value of n varies widely from study to study (15, 20), because it depends on the minimum size of the ejecta that is capable of sustaining life (or molecular material) and many other biological and dynamical considerations. However, even for the conservative choice of $E = 1.01$ and $n \sim 10^3$, it follows that $P_a/P_0 \sim 10^4$. If we compare the relative probabilities for any of the TRAPPIST-1 habitable planets and the Earth, assuming E to be the same in both instances, we find

$$\frac{P_a^{(T)}}{P_a^{(E)}} = E^{n(T)-n(E)} \approx E^{n(T)}, \qquad [8]$$

where the last equality follows from our argument that panspermia events are likely to be much more common on TRAPPIST-1. Although we cannot hope to estimate E or $n(T)$, a robust qualitative conclusion can be drawn: the presence of an exponential scaling on the RHS of Eq. **8** ensures that the probability of abiogenesis via panspermia can be orders of magnitude higher than on Earth in the optimal limit.

Analogies with Ecological Models

The close proximity of the TRAPPIST-1 planets is reminiscent of an analogous environment (albeit at much smaller scales) on the Earth, namely islands. If we look on the habitable planets of

the TRAPPIST-1 system as "islands," the similarities are readily apparent: although these islands are isolated to a degree, they are also subject to "immigration" from the "mainland." In planetary terms, this immigration would essentially amount to transfer of lifeforms (or genetic material) via panspermia. The only difference is that islands occupy a 2D surface and planets occupy a 3D volume, but most of the relevant orbits in the latter case share a common plane.

This analogy enables us to draw on the rich and versatile field of island biogeography (27, 28), which primarily arose from the seminal paper in ref. 29. (In ref. 30, the theory of island biogeography was used to qualitatively explore the possibility that photosynthesis could be transferred via interplanetary panspermia.) The basic insight of refs. 27 and 29 was that there exists a dynamic equilibrium between the immigration ($\mathcal{I}$) and extinction ($\mathcal{E}$) rates on the island, which determines the equilibrium number of species. Ref. 29 had hypothesized that

$$\mathcal{I} \propto A_x R_y \frac{\exp\left(-\lambda D_{xy}\right)}{D_{xy}}, \qquad [9]$$

where A_x is the area of the "source" from which immigration occurs, R_y is the diameter of the island, D_{xy} is the distance between the source and the island, and λ represents a characteristic inverse scale length. If we consider the Earth–Mars and TRAPPIST-1 systems, it is apparent that $\mathcal{I}$ will be much higher for the latter case because of the smaller value of D_{xy}. The expression for $\mathcal{E}$ is more ambiguous, but it suffices to say that it increases as the area of the island decreases. Thus, compared with Mars, the extinction rate is likely to be lower for the TRAPPIST-1 system.

The species diversity $\mathcal{S}$ is expressible as

$$\frac{d\mathcal{S}}{dt} = \mathcal{I}\left(\mathcal{S}_P - \mathcal{S}\right) - \mathcal{E}\mathcal{S}, \qquad [10]$$

and the equilibrium species diversity $\mathcal{S}_\star$ is thus given by

$$\mathcal{S}_\star = \mathcal{S}_P \frac{\mathcal{I}}{\mathcal{I}+\mathcal{E}}, \qquad [11]$$

where $\mathcal{S}_P$ is the total number of species capable of migrating from the source (31). Thus, we see that $\mathcal{S}_\star$ increases with respect to $\mathcal{S}_P$ and $\mathcal{I}$ and decreases with respect to $\mathcal{E}$. Because $\mathcal{I}$ is much higher and $\mathcal{E}$ is slightly lower for the TRAPPIST-1 system, it follows that the species diversity will be much higher than in the Earth–Mars case, provided that the values of $\mathcal{S}_P$ are similar. Hence, the TRAPPIST-1 planets seeded by panspermia are characterized by a greater number of species thus transferred compared with the solar system.

The similarities between the TRAPPIST-1 system and ecological models extend beyond island biogeography. Another important paradigm in theoretical ecology is the concept of a metapopulation, which is commonly referred to as a "population of populations" (32). Additional details concerning metapopulation ecology can be found in refs. 33 and 34. Let us now couch the TRAPPIST-1 system in terms of metapopulations.

The central premise is that the metapopulation (planetary system) is made up of different "patches" (planets). We suppose that the total number of distinct populations (life-bearing planets) is $\mathcal{N}$, which has a governing equation of

$$\frac{d\mathcal{N}}{dt} = \mathcal{I}\mathcal{N}\left(1 - \frac{\mathcal{N}}{\mathcal{N}_T}\right) - \mathcal{E}\mathcal{N}, \qquad [12]$$

where $\mathcal{N}_T$ is the total number of sites available (number of HZ planets), whereas $\mathcal{I}$ and $\mathcal{E}$ are the immigration and extinction rates, respectively. For the equilibrium number $\mathcal{N}_\star$, we find that

$$\mathcal{N}_\star = \mathcal{N}_T\left(1 - \frac{\mathcal{E}}{\mathcal{I}}\right). \qquad [13]$$

This result implies that $\mathcal{N}_\star$ increases monotonically with $\mathcal{N}_T$ and $\mathcal{I}$ and decreases monotonically with $\mathcal{E}$. Using the information presented earlier, we conclude that the TRAPPIST-1 system is consistent with a greater number of life-bearing planets because of the higher immigration rates and total number of available planets (in the HZ) compared with the solar system.

The aforementioned mathematical models are very useful in deducing qualitative or semiquantitative statements about the TRAPPIST-1 system. Beyond the two analogies explored here, a promising and diverse array of formalisms and concepts introduced in theoretical ecology (35–39) is capable of furthering our understanding of panspermia and abiogenesis in multiplanetary systems.

Implications of Panspermia

Finally, we explore some of the major consequences arising from our analysis.

Detecting the Existence of Panspermia. We have stated earlier that the probability of abiogenesis increases from a value of P_0 without panspermia to Eq. **7** if panspermia is present. Suppose that we detect k planets in the TRAPPIST-1 system with signs of life, typically via molecular biosignatures in the planets' atmospheres (8). The probability of abiogenesis occurring independently on them would be P_0^k, whereas it could equal P_a^k if all planets exchange material with each other. Because the ratio $\left(P_a/P_0\right)^k$ is plausibly much greater than unity for $k \geq 1$, detecting life on two (or more) planets strengthens the case for abiogenesis via panspermia. Other statistical metrics proposed for distinguishing between the cases of null and finite panspermia (40, 41) are also useful in this context.

Another means of detecting lifeforms is through the "red edge" of vegetation, which corresponds to a sharp increase in the reflectance at around 0.7 μm on the Earth (42). Thus, if the red edge is detected through photometric observations on two (or more) different planets, at the same wavelength, it would strengthen the case for panspermia. Because TRAPPIST-1 is an ultracool dwarf star, its peak blackbody brightness is at 1.1 μm. Hence, any searches for the red edge must be cognizant of the possibility that it may be shifted to longer wavelengths than on Earth (43). Due care must also be taken to identify false positives, such as minerals and other "artificial" spectral edges.

Life as we know it is characterized by homochirality (i.e., living organisms utilize left-handed amino acids and right-handed sugars). Homochirality has been posited to be a universal feature of biochemical life and can be detected via remote sensing using circular polarization spectroscopy (44). Hence, the discovery of homochirality on multiple planets may further serve as a means of differentiating between panspermia and independent abiogenesis.

To summarize, the transfer of life via panspermia can be tested by determining whether the same biosignatures are detected on multiple planets. Consequently, this fact can also be used to study the sensitivity of life to initial conditions, such as the illumination, surface gravity, atmospheric pressure, and other factors.

Looking Beyond TRAPPIST-1. Although most of our discussion was centered around TRAPPIST-1, many of the conclusions discussed herein have a broader scope.

M dwarfs. Consider a generic multiplanet system around an M dwarf, where multiple planets are within the HZ. From figure 7 of ref. 45, we infer that the width of the HZ is around 0.03–0.05 a.u. for a star of 0.1–0.2 $M_\odot$. If there exist more than one planet in this region, we conclude that $D_{xy} \sim a_y \sim \mathcal{O}\left(10^{-2}\right)$ a.u. We can then estimate the relative fraction of rocks that are transferred compared with the Earth-to-Mars scenario using Eq. **3**, thereby obtaining

$$\frac{P_{xy}}{P_{EM}} \approx 20 \left(\frac{\eta_{xy}}{\eta_{EM}}\right) \left(\frac{M_y}{M_\oplus}\right)^{\frac{2}{3}} \left(\frac{M_\star}{0.1\, M_\odot}\right)^{-\frac{2}{3}}, \qquad [14]$$

where $P_{EM} = 2 \times 10^{-3}$ (13). Thus, for most M-dwarf systems, the fraction of rocks impacting the target planet is conceivably around an order of magnitude higher than the Earth-to-Mars value. Using Eq. **4**, we conclude that

$$\frac{\tau_{xy}}{\tau_{EM}} \approx 0.007 \left(\frac{D_{xy}}{0.01\ \text{a.u.}}\right) \left(\frac{\langle v_{EM}\rangle}{\langle v\rangle}\right), \qquad [15]$$

with $\tau_{EM} = 4.7$ My (13), implying that the transit time is two (or more) orders of magnitude lower compared with the Earth-to-Mars value. Collectively, Eqs. **14** and **15** would result in higher immigration rates, which imply that our previous ecology-based results are likely to be valid.

Exomoons. A second analogous setup involves a planet with multiple exomoons in the circumplanetary HZ. Habitable exomoons cannot exist over long timescales when the star's mass is $< 0.5\ M_\odot$, because their orbits are rendered dynamically unstable (46). Nonetheless, this case should be evaluated on the same footing as M-dwarf planetary systems, because habitable exomoons may even outnumber habitable exoplanets (47) and will soon be detectable by forthcoming observations (48). Most of our analysis will still be applicable, except for the fact that the exoplanets and star must be replaced by exomoons and exoplanet, respectively.

To gain an estimate of the relative increase in probability with respect to the Earth-to-Mars case, let us make use of Eqs. **14** and **15**. Suppose that $M_y \sim 0.1\ M_\oplus$, $M_\star \sim 10^{-2} M_\odot$, and $D_{xy} \sim 0.01$ a.u. using parameters consistent with ref. 47; we also assume $\eta_{xy} \sim \eta_{EM}$ and $\langle v\rangle \sim \langle v_{EM}\rangle$. With these choices, we find $P_{xy}/P_{EM} \approx 20$ and $\tau_{xy}/\tau_{EM} \approx 0.007$, which equal the characteristic values obtained for low-mass M-dwarf planetary systems. Thus, exomoon systems in the circumplanetary HZ are conducive to panspermia, with all other things held equal. This result also implies a greater degree of biodiversity and a higher number of moons seeded by panspermia as per our earlier arguments.

Brown dwarfs. As seen from Eq. **3**, the capture probability has an $M_\star^{-2/3}$ dependence. If we assume that there exist multiple habitable planets around a brown dwarf, the low value of $M_\star$ relative to the Sun could, theoretically speaking, enhance the probability of panspermia. However, the HZ around brown dwarfs migrates inward over time (49), thereby diminishing the chances for abiogenesis and panspermia to occur.

Discussion and Conclusions

In this paper, we addressed the important question of whether life can be transferred via rocks (lithopanspermia) in the TRAPPIST-1 system. By formulating a simple model for lithopanspermia, we showed that its likelihood is orders of magnitude higher than the Earth-to-Mars value because of the higher capture probability per impact event and the much shorter transit timescales involved.

We explored the implications of panspermia for the origin of life in the TRAPPIST-1 system by drawing on the quantitative approach proposed recently in ref. 24. If panspermia (or pseudopanspermia) is an effective mechanism, it leads to a significant boost in the probability of abiogenesis because each panspermia event can transfer a modest number of molecular species, and the cumulative probability scales exponentially in the best case scenario. Thus, it seems reasonable to conclude that the chances for abiogenesis are higher in the TRAPPIST-1 system compared with the solar system.

We also benefited from the exhaustive field of theoretical ecology in substantiating our findings. By drawing on the analogy with the theory of island biogeography, we argued that a large number of species could have "immigrated" from one planet to another, thereby increasing the latter's biodiversity. As known from studies on Earth, a higher biodiversity is correlated with greater stability (50), which bodes well for the multiple members of the TRAPPIST-1 system. We also used metapopulation ecology to conclude that the possibility of multiple planets being "occupied" (i.e., bearing life) is higher than in the solar system given the considerably higher immigration rates.

To observationally test the presence of life seeded by panspermia, we proposed a couple of general tests that can be undertaken in the future. We reasoned that a "smoking gun" signature for panspermia may require the following criteria to be valid: (*i*) the detection of identical biosignature gases, (*ii*) the spectral red edge feature of vegetation occurring at the same wavelength, and (*iii*) the existence of distinctive homochirality. However, we predict that some of these observations may only fall within the capabilities of future telescopes, such as the Large UV/Optical/Infrared Surveyor (https://asd.gsfc.nasa.gov/luvoir/).

Lastly, we extended our discussion beyond that of the TRAPPIST-1 system and presented other scenarios where panspermia and hence, abiogenesis are more likely than in the solar system. We identified exoplanetary systems orbiting lower-mass M dwarfs (and perhaps, brown dwarfs) and exomoons around Jovian-sized planets as potential candidates that favor panspermia.

It seems likely that exoplanetary systems akin to TRAPPIST-1, with multiple exoplanets closely clustered in the HZ, will be discovered in the future. We anticipate that our work will be applicable to these exotic worlds vis-à-vis the greater relative probability of panspermia and abiogenesis on them.

ACKNOWLEDGMENTS. We thank James Benford, Sebastiaan Krijt, Amaury Triaud, and Ed Turner for their helpful comments regarding the manuscript. This work was partially supported by a grant from the Breakthrough Prize Foundation for the Starshot Initiative.

1. Winn JN, Fabrycky DC (2015) The occurrence and architecture of exoplanetary systems. *Annu Rev Astron Astrophys* 53:409–447.
2. Lammer H, et al. (2009) What makes a planet habitable? *Astron Astrophys Rev* 17:181–249.
3. Dressing CD, Charbonneau D (2015) The occurrence of potentially habitable planets orbiting M dwarfs estimated from the full Kepler dataset and an empirical measurement of the detection sensitivity. *Astrophys J* 807:45.
4. Shields AL, Ballard S, Johnson JA (2016) The habitability of planets orbiting M-dwarf stars. *Phys Rep* 663:1–38.
5. Anglada-Escudé G, et al. (2016) A terrestrial planet candidate in a temperate orbit around Proxima Centauri. *Nature* 536:437–440.
6. Gillon M, et al. (2016) Temperate Earth-sized planets transiting a nearby ultracool dwarf star. *Nature* 533:221–224.
7. Gillon M, et al. (2017) Seven temperate terrestrial planets around the nearby ultracool dwarf star TRAPPIST-1. *Nature* 542:456–460.
8. Seager S, Bains W, Petkowski JJ (2016) Toward a list of molecules as potential biosignature gases for the search for life on exoplanets and applications to terrestrial biochemistry. *Astrobiology* 16:465–485.
9. Melosh HJ (1988) The rocky road to panspermia. *Nature* 332:687–688.
10. Gladman BJ, Burns JA, Duncan M, Lee P, Levison HF (1996) The exchange of impact ejecta between terrestrial planets. *Science* 271:1387–1392.
11. Burchell MJ (2004) Panspermia today. *Int J Astrobiol* 3:73–80.
12. Wesson PS (2010) Panspermia, past and present: Astrophysical and biophysical conditions for the dissemination of life in space. *Space Sci Rev* 156:239–252.
13. Worth RJ, Sigurdsson S, House CH (2013) Seeding life on the moons of the outer planets via lithopanspermia. *Astrobiology* 13:1155–1165.
14. Opik EJ (1951) Collision probability with the planets and the distribution of planetary matter. *Proc R Ir Acad A Math Phys Sci* 54:165–199.
15. Mileikowsky C, et al. (2000) Natural transfer of viable microbes in Space. 1. From Mars to Earth and Earth to Mars. *Icarus* 145:391–427.
16. Gladman B, Dones L, Levison HF, Burns JA (2005) Impact seeding and reseeding in the inner solar system. *Astrobiology* 5:483–496.
17. Steffen JH, Li G (2016) Dynamical considerations for life in multi-habitable planetary systems. *Astrophys J* 816:97.
18. Housen KR, Schmidt RM, Holsapple KA (1983) Crater ejecta scaling laws - Fundamental forms based on dimensional analysis. *J Geophys Res* 88:2485–2499.
19. Neukum G, Ivanov BA, Hartmann WK (2001) Cratering records in the inner solar system in relation to the lunar reference system. *Space Sci Rev* 96:55–86.

20. Nicholson WL (2009) Ancient micronauts: Interplanetary transport of microbes by cosmic impacts. *Trends Microbiol* 17:243–250.
21. Horneck G, Klaus DM, Mancinelli RL (2010) Space microbiology. *Microbiol Mol Biol Rev* 74:121–156.
22. Lineweaver CH, Davis TM (2002) Does the rapid appearance of life on Earth suggest that life is common in the universe? *Astrobiology* 2:293–304.
23. Spiegel DS, Turner EL (2012) Bayesian analysis of the astrobiological implications of life's early emergence on Earth. *Proc Natl Acad Sci USA* 109:395–400.
24. Scharf C, Cronin L (2016) Quantifying the origins of life on a planetary scale. *Proc Natl Acad Sci USA* 113:8127–8132.
25. Orgel LE (2004) Prebiotic chemistry and the origin of the RNA world. *Crit Rev Biochem Mol Biol* 39:99–123.
26. Nisbet EG, Sleep NH (2001) The habitat and nature of early life. *Nature* 409:1083–1091.
27. MacArthur RH, Wilson EO (2001) *The Theory of Island Biogeography*, Princeton Landmarks in Biology (Princeton Univ Press, Princeton), Vol 1.
28. Whittaker RJ, Fernández-Palacios JM (2007) *Island Biogeography: Ecology, Evolution, and Conservation* (Oxford Univ Press, London).
29. MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. *Evolution* 17:373–387.
30. Cockell CS (2008) The interplanetary exchange of photosynthesis. *Orig Life Evol Biosph* 38:87–104.
31. Diamond JM (1972) Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest pacific islands. *Proc Natl Acad Sci USA* 69:3199–3203.
32. Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240.
33. Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49.
34. Hanski I (1999) *Metapopulation Ecology* (Oxford Univ Press, London).
35. Dias PC (1996) Sources and sinks in population biology. *Trends Ecol Evol* 11:326–330.
36. McGill BJ, et al. (2007) Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecol Lett* 10:995–1015.
37. Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*, Monographs in Population Biology (Princeton Univ Press, Princeton), Vol 32.
38. Chase JM, Leibold MA (2003) *Ecological Niches* (Univ of Chicago Press, Chicago).
39. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
40. Lin HW, Loeb A (2015) Statistical signatures of panspermia in exoplanet surveys. *Astrophys J Lett* 810:L3.
41. Lingam M (2016) Interstellar travel and galactic colonization: Insights from percolation theory and the yule process. *Astrobiology* 16:418–426.
42. Seager S, Turner EL, Schafer J, Ford EB (2005) Vegetation's red edge: A possible spectroscopic biosignature of extraterrestrial plants. *Astrobiology* 5:372–390.
43. Kiang NY, et al. (2007) Spectral signatures of photosynthesis. II. Coevolution with other stars and the atmosphere on extrasolar worlds. *Astrobiology* 7:252–274.
44. Sparks WB, et al. (2009) Detection of circular polarization in light scattered from photosynthetic microbes. *Proc Natl Acad Sci USA* 106:7816–7821.
45. Kopparapu RK, et al. (2013) Habitable zones around main-sequence stars: New estimates. *Astrophys J* 765:131.
46. Sasaki T, Barnes JW (2014) Longevity of moons around habitable planets. *Int J Astrobiol* 13:324–336.
47. Heller R, et al. (2014) Formation, habitability, and detection of extrasolar moons. *Astrobiology* 14:798–835.
48. Peters MA, Turner EL (2013) On the direct imaging of tidally heated exomoons. *Astrophys J* 769:98.
49. Barnes R, Heller R (2013) Habitable planets around white and brown dwarfs: The perils of a cooling primary. *Astrobiology* 13:279–291.
50. Hooper DU, et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr* 75:3–35.