



## SYMPOSIUM

# The Ecomechanics of Gecko Adhesion: Natural Surface Topography, Evolution, and Biomimetics

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**Synopsis** The study of gecko adhesion is necessarily interdisciplinary due to the hierarchical nature of the adhesive system and the complexity of interactions between the animals and their habitats. In nature, geckos move on a wide range of surfaces including soft sand dunes, trees, and rocks, but much of the research over the past two decades has focused on their adhesive performance on artificial surfaces. Exploring the complex interactions between geckos and their natural habitats will reveal aspects of the adhesive system that can be applied to biomimetic research, such as the factors that facilitate movement on dirty and rough surfaces with varying microtopography. Additionally, contrasting suites of constraints and topographies are found on rocks and plants, likely driving differences in locomotion and morphology. Our overarching goals are to bring to light several aspects of ecology that are important for gecko–habitat interactions, and to propose a framework for how they can inspire material scientists and functional ecologists. We also present new data on surface roughness and topography of a variety of surfaces, and adhesive performance of *Phelsuma* geckos on surfaces of varying roughness. We address the following key questions: (1) why and how should ecology be incorporated into the study of gecko adhesion? (2) What topographical features of rocks and plants likely drive adhesive performance? (3) How can ecological studies inform material science research? Recent advances in surface replication techniques that eliminate confounding factors among surface types facilitate the ability to address some of these questions. We pinpoint gaps in our understanding and identify key initiatives that should be adopted as we move forward. Most importantly, fine details of locomotor microhabitat use of both diurnal and nocturnal geckos are needed.

## Introduction

Understanding what factors drive diversification and complexity of function in real ecosystems has been a recent driving force in eco-evolutionary dynamics (Bellwood et al. Forthcoming 2019; Meester et al. 2019). This move to place a more functional slant on ecological studies must be matched by the incorporation of a more ecological relevance in studies of function. Many biomechanically-based evolutionary novelties are primarily examined in an artificial laboratory setting with little regard to ecological

context. A prime example of this is the adhesive apparatus of geckos, which has been the focus of hundreds of studies over the past two decades although only a small fraction of them have incorporated, or even mentioned, anything about the natural habitat of geckos (Niewiarowski et al. 2016).

Geckos are remarkably diverse (about 1855 species) and it is perhaps not surprising that many types of habitats/surfaces are occupied by them, such as trees, shrubs, dunes, soils, sandplains, termite mounds, rodent burrows, beaches, savannah, caves,

mines, and human-made structures (Storr et al. 1990; Geniez et al. 2004; Spawls et al. 2004; Grismer 2011; Cogger 2014; Marques et al. 2018; Fig. 1). Accompanying this diversity in ecology is a variable compendium of pedal specializations, including webbed feet, paraphalanges, and adhesive toe pads (Bauer and Russell 1991; Higham 2015) thought to enhance particular organism–substrate interactions. Adhesive toe pads originated as early as the mid-Cretaceous (Bauer 2019), highlighting their persistence. Geckos are, therefore, an extraordinary group for exploring the eco-evolutionary dynamics of complex biomechanical systems.

Gecko adhesion has long been recognized as a surface interaction phenomenon (Home 1816) and various hypotheses have been advanced, tested and, in most cases, rejected as explanations of how such attachment works (Home 1816; Wagler 1830; Cartier 1872; Simmermacher 1884; Haase 1900; Gadow 1901; Weitlaner 1902; Kunitzky 1903; Schmidt 1905, 1913; Hora 1923; Dellit 1934; Mahendra 1941; Altevogt 1954; Maderson 1964; Hiller 1968). The “drilling down” to elucidate the functional attributes of individual setae has revealed a great deal about the attachment phenomenon and its potential applications, but has been accomplished almost entirely in the absence of an understanding of how and when geckos employ this remarkable property in nature. Maderson (1970) lamented that we know little about the adaptive value of the adhesive capabilities of geckos in their natural environments, and the intervening 50 years have not substantially rectified this. Indeed, until relatively recently the only attempts to elucidate this were focused on a dwarf, leaf-litter dwelling gecko with miniscule toe pads (Gasc and Renous 1980; Gasc et al. 1982).

Studies of gecko adhesion exhibit two main inconsistencies: whether the substrates used were natural or not, and whether locomotion (or just static adhesion) was measured on those surfaces. At the whole organism level adhesive capacity has been quantified for geckos on a variety of artificial smooth (Hiller 1968; Irschick et al. 1996; Autumn et al. 2000; Peressadko and Gorb 2004; Stewart and Higham 2014; Higham et al. 2017a) and very fine-grained rough (Campolo et al. 2003; Persson 2003; Persson and Gorb 2003) surfaces. At a coarser roughness level Vanhooydonck et al. (2005) found that locomotor performance in a pad-bearing gecko was diminished on canvas, plywood, and wire mesh, compared with a smooth surface, but they did not measure clinging ability or surface characteristics. In contrast, Gillies et al. (2014) measured clinging

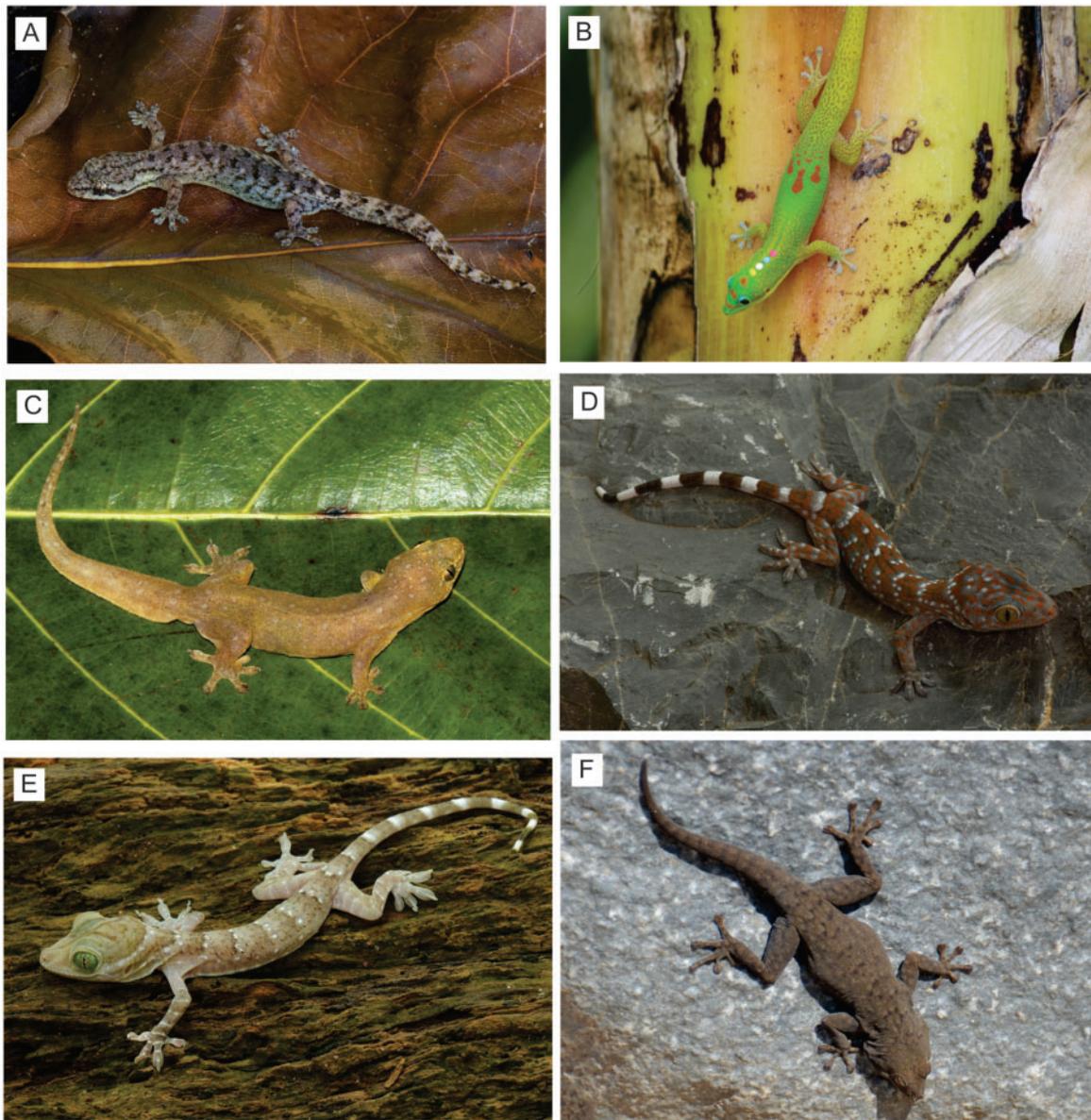
ability of Tokay geckos (*Gekko gecko*) on a variety of macroscopically rough engineered surfaces, and found that shear adhesion was significantly diminished on surfaces with amplitudes and wavelengths similar to the animal’s lamella length and interlamella distance, nicely highlighting the importance of considering length-scale, and identifying the importance of toepad compliance and passive conformation ability (Gillies et al. 2014). The surfaces used, however, were not naturally occurring and locomotor ability was not measured.

There is, therefore, a gap in our knowledge between our understanding of seta-based adhesion at the level of individual fibrils and how this translates into whole animal adhesive performance on routinely used naturally-occurring substrata. One variable that has received attention in this regard is surface roughness. It is evident that some geckos routinely use highly irregular surfaces (e.g., Loveridge 1947; Russell 1976; Espinoza et al. 1990; Collins et al. 2015) that are qualitatively quite different from the smooth and microscopically rough artificial surfaces employed in laboratory investigations of gecko adhesion and clinging ability.

Herein we address the importance of incorporating ecological parameters when studying gecko adhesion. We explore the potential variation that can be observed on rock and plant surfaces exploited by geckos, and the ways in which we can begin to quantify their microtopography. We examine what is known about geckos resting or moving on natural surfaces, and supplement this with insights from research on insects and arachnids. We address the importance of field observations and enclosure experiments. Following a discussion of the replication of natural surfaces, which can only be entered into when those surfaces have been identified in nature, we provide a framework for connecting ecomechanics, biomimetics, and evolution.

## Why incorporate ecology into the study of gecko adhesion?

Despite major advancements in the understanding of gecko adhesion since the turn of the millennium (Autumn et al. 2000), only a few attempts have been made to rigorously incorporate an ecological component (Niewiarowski et al. 2016). Doing so enables us to identify the context for the origin of adhesion, and the shift from low levels of adhesion to very high levels (Fig. 2). An ecological framework is also necessary for understanding gecko diversity and to ask questions about constraints on, and promoters of, evolution. Are certain surfaces amenable



**Fig. 1** Photos of geckos on different types of substrate. **A)** *Hemiphyllodactylus mgmyinti* on a dead leaf, **B)** *Phelsuma laticauda* on a smooth banana trunk, **C)** *Gehyra mutilata* on a fresh leaf, **D)** *Gekko gekko* on a rock, **E)** *Gekko smithii* on a rough tree trunk, **F)** *Rhoptropus bradfieldi* on a dolerite boulder in Namibia. Photos from A, C, D, and E are from Lee Grismer; B is from A.W., and F is from T.E.H.

to geckos with adhesive capabilities, but not to other species of lizard? If so, this might promote diversification.

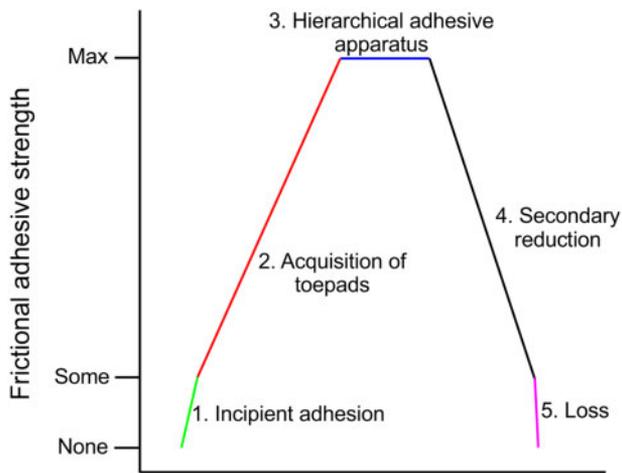
### Ecological scenarios for the origin and elaboration of adhesive capabilities

#### Origin

The origin of gecko adhesion is challenging to address as most pad-bearing geckos have a fully-developed system that develops extremely high shear adhesive strength. However, there are cases where adhesion is evident with only the rudiments of toe pads being present. Such cases provide a window into the origin

of adhesion and the associated ecological context (Fig. 2). *Gonatodes* is a prime example of a genus in which adhesion is associated with incipient toe pads. Most species of this genus are incapable of generating measurable adhesive force (Higham et al. 2017a), but *Gonatodes humeralis* is unique in having branched setae and adhesive capabilities (Russell et al. 2015; Higham et al. 2017a), and can ascend a vertical sheet of smooth acrylic, an impressive feat for a gecko without well-developed toepads (Higham et al. 2017a).

What selective pressures may favor the transformation of spinules (tiny hair-like growths) into adhesive setae? One scenario involves the opening up of new areas of a habitat (smoother and higher),



**Fig. 2** A schematic showing the different states and hypothetical transitions between different levels of gecko adhesion. The x-axis could represent evolutionary time. 1. Incipient adhesion is the transition from no adhesive abilities to an amount suitable for moving up vertical smooth surfaces, as in *Gonatodes humeralis* (Higham et al. 2017a). 2. The acquisition of toepads, which likely stems from the response to momentary demands imposed on the adhesive system for the ability to generate extremely high frictional adhesive forces (Higham et al. 2017b). 3. The maintenance of a fully-developed hierarchical adhesive apparatus (e.g., *G. gecko*), which is the state most commonly studied when examining adhesion. 4. Secondary reduction of adhesive capacity and structure that appears to be connected to shifts to a life on relatively flat ground, as in *Rhoptropus afer* (Higham et al. 2015), and 5. Complete loss of the adhesive apparatus, as in some dune-dwelling geckos (Bauer and Russell 1991).

allowing geckos to avoid competition by partitioning resources. Having the ability to increase friction would potentially enable a gecko to remain stationary on a smooth leaf surface when sleeping. Indeed, *G. humeralis* has been observed resting on smooth leaf surfaces (Murphy 1997), and sleeping at night on leaves (Avilla-Pires 1995). In Trinidad, *G. humeralis* frequently occupies vertical smooth bamboo shoots, a challenging substrate that is not occupied by other lizards (Higham et al. 2017a). Individuals of this species move very little (2.3% of observation time) and perch with their head down the majority (68%) of the time (Persaud et al. 2003). This posture is compatible with a directional adhesive and with a reduction in energy expenditure. There is strong evidence for pad-bearing lizards dividing resources in their habitat (Harmon et al. 2007; Noble et al. 2011), and these are often accompanied by morphological, performance, or behavioral shifts. If function is altered significantly, what impact might such newly-acquired capabilities have on microhabitat use and biogeography? *Gonatodes humeralis* has a much larger geographic range than any of its congeners,

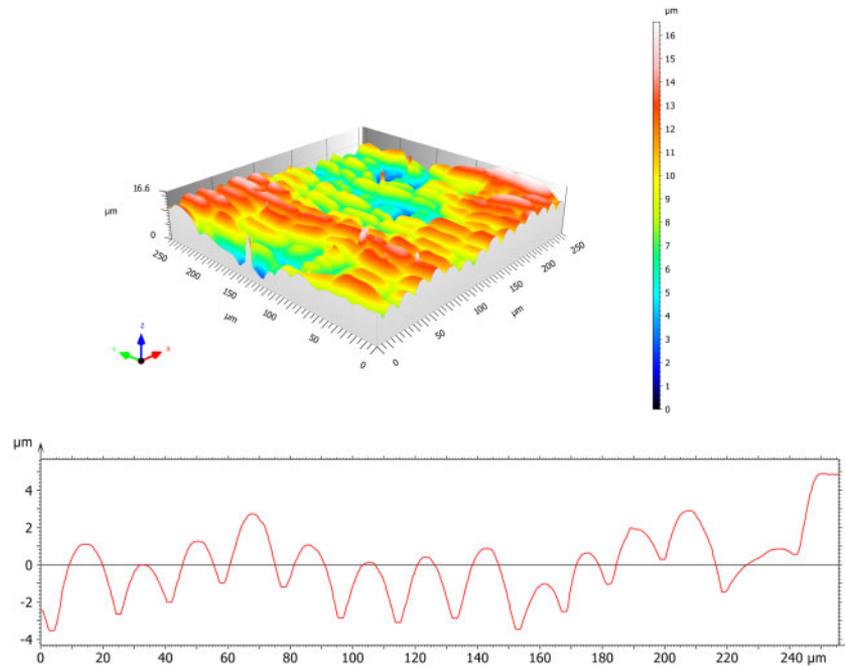
and exhibits one of the largest native ranges of any gecko species (Meiri et al. 2017; Roll et al. 2017). It is possible that its large range is associated with its ability to adhere, and this may be a precursor to diversification (Pinto et al. 2019).

### Elaboration of the system: are geckos overbuilt?

The example above of *G. humeralis* shows that only small shifts in morphology are necessary to attain substantive adhesive capabilities. However, when the adhesive strength of single setae was first quantified, followed by the scaling up to the total toe-pad area, pad-bearing geckos appeared to be able to generate more force than would ever be necessary for their own requirements. In fact, calculated safety factors for static clinging can approach or exceed 100 (Irschick et al. 1996; Higham et al. 2017a). This leads to an obvious question: Why have many groups of geckos evolved elaborate hierarchical adhesive systems incorporating many internal and external morphological changes (Russell 1979, 1981; Russell and Bauer 1988, 2008), and biomechanical shifts (Zaaf et al. 2001; Russell and Higham 2009) to generate seemingly unnecessary force? The answer may not be related to what geckos do routinely, but rather what geckos do on rare occasions. In addition to the fact that roughness itself is present on many different length scales (thus necessitating the hierarchical system—see Persson 2007), several observations reveal that many species of gecko jump or fall from trees (up to 15 m) to escape predation (Taylor 1922; Anderson 1964; Minton 1966; Bauer 1990; Vitt and Zani 1997), and may catch a leaf or other structure to arrest the fall. A recent study used mathematical modeling to estimate the impact forces of geckos landing on leaves with different surface areas (Higham et al. 2017b). In all cases, impact forces were quite high, with dynamic safety factors (maximum frictional adhesive force divided by impact force) often falling below 4 and sometimes falling below 1. This momentarily excessive force has the potential to shape evolution and select for higher adhesive force, despite being rarely exploited (Gans 1979). Real-world challenges to the adhesive system also occur when geckos move on natural surfaces, such as rocks and plants. These are discussed below.

### Surface roughness and why it matters

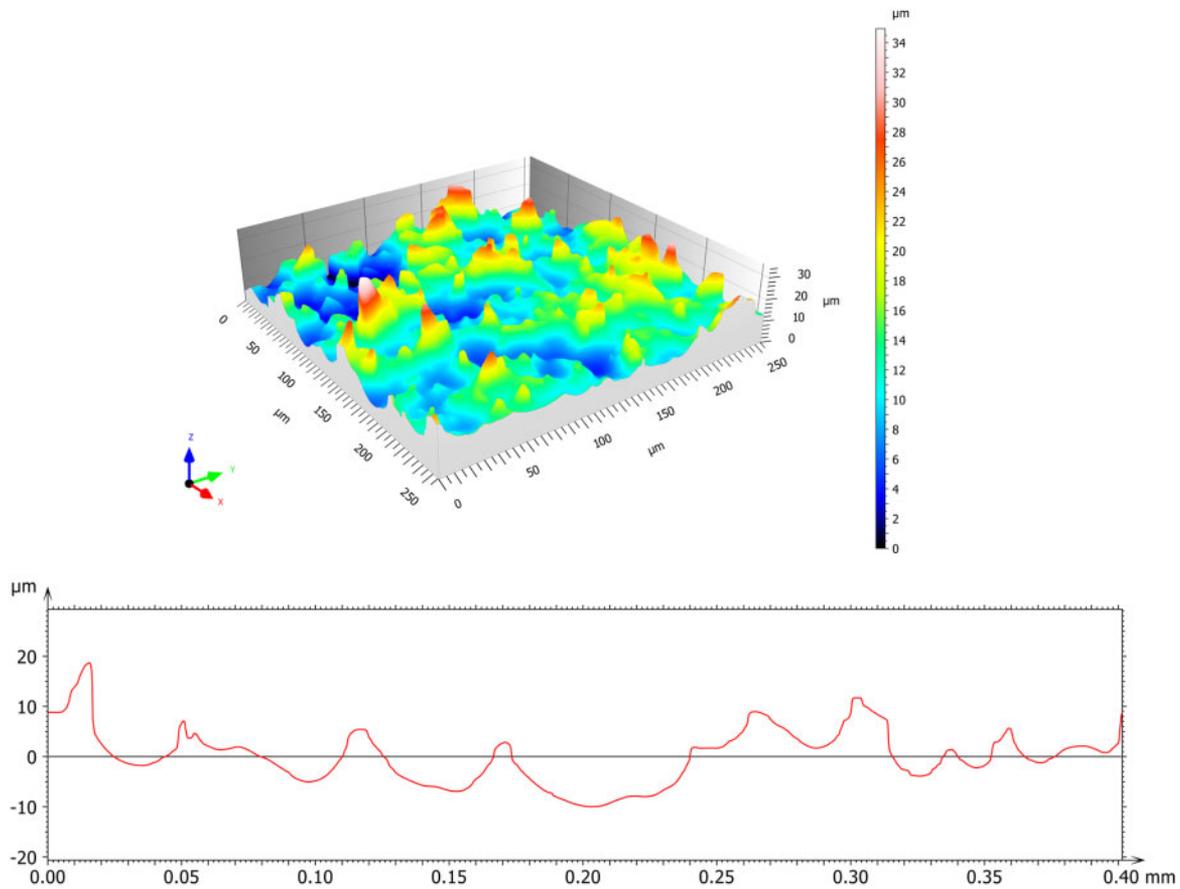
Even though surface roughness is of fundamental importance to adhesion between gecko toe pads and the surfaces they use (Russell and Johnson 2007), we actually know very little about the practical constraints that limit gecko adhesive performance



**Fig. 3** Example of the 3D surface microtopography of the adaxial surface of a banana leaf (*Musa*), with warmer colors denoting higher peaks. Image created in MountainsMap Premium 7.2 (Digital Surf, France). Below the image is a single line profile showing the amplitude and spacing between asperities.

on either natural or synthetic substrates. The dearth of studies quantifying substrate use by free-ranging geckos, and the focus of most laboratory studies on adhesive performance on atypically smooth substrates (e.g., glass) is only part of the problem. A more fundamental challenge involves the technical and theoretical difficulties involved in characterizing the roughness of surfaces in general (Persson et al. 2018). Adhesion to rough surfaces arises from attraction between atoms of the gecko skin and atoms of the contacted surface, possible only with elastic deformation of the materials which permits less than nanometer separation. However, surface roughness can extend over many length scales that are relevant to making contact at the smallest scales. Indeed, tribologists and metrologists have labored for decades to develop techniques to characterize roughness, and to formulate theory to distill a manageable set of parameters relevant to predicting aspects of surface performance that are roughness dependent (Gujrati et al. 2018). By and large, surface roughness is measured at different length scales using stylus profilometry, atomic force microscopy (AFM), and optical profilometry (Jacobs et al. 2017). Choice of instrument/technique is determined by the length scale of measurement possible and resolution desired. Approaches are being developed that can combine techniques for single surfaces, allowing continuous measurement of up to eight orders of magnitude (Gujrati et al. 2018).

Although most studies of gecko (and other animals) adhesion reference a single summary statistic of surface roughness (e.g., root mean square [RMS] roughness), it is important to recognize that these are likely inadequate (especially for natural surfaces) for the comparative or theoretical purposes related to predicting or explaining its effects on adhesion (Jacobs et al. 2017). RMS roughness is a standardized measure of the variance in profile height from the centerline average of a surface (Halling 1978), and will depend on the length scale. Referring to the surface profiles shown in Figs. 3 and 4 reveals why RMS, although a straightforward description of variation in the heights of peaks and valleys of a surface, masks other characteristics of surface topography that are likely relevant to adhesion (such as spacing and shape). Complete characterizations of surfaces are possible using techniques that capture the full 3D aspects of asperities (called roughness power spectra, PSD), from which parameters such as RMS can be recovered. However, in practice, surface characterization data are difficult to collect, and as a thorough review by Jacobs et al. (2017) explains, there are both practical and theoretical challenges to constructing PSDs from measurements of real surfaces. Three classes of challenges discussed are (1) variation in methods of PSDs computation that impact numerical results, (2) assumptions associated with measurement or experimental limitations can lead to biased or incomplete PSDs, and



**Fig. 4** Example of the 3D surface microtopography of 600 grit-sandpaper, with warmer colors denoting higher peaks. Image created in MountainsMap Premium 7.2 (Digital Surf, France). Below the image is a single line profile showing the amplitude and spacing between asperities. Note the difference in scale between this profile and that depicted in Fig. 3.

(3) instrument and analysis artifacts in characterizing surfaces at the very smallest length scales must be detected and mitigated. While it may not be clear how any of the challenges above individually or in combination relate to limitations in predicting the adhesion of geckos on the kinds of surfaces they actually use, until we develop methods to identify and then characterize all the relevant dimensions of surface roughness for the gecko adhesive system, we may be practically limited to using one dimensional measures such as RMS. We believe it remains an open question as to whether measures such as RMS, which may be appropriate for studies of adhesion on synthetic surfaces prepared with identical methods (Bhushan 2000), can help narrow down parameters of interest that must be included in the characterization of surfaces used by free-ranging geckos.

Simple measures of roughness can be quantified in either two- or three-dimensions, with the latter becoming increasingly important (Gadelmawla et al. 2002). Three-dimensional roughness parameters incorporate a series of 2D profiles, measured across the

surface of a sample (Gadelmawla et al. 2002; Kumar et al. 2019). Of the parameters that can be measured, those that quantify the vertical characteristics of surface deviations are the most commonly employed. These include the arithmetic average height parameter ( $R_a$ ), also termed the center line average, which is the average absolute deviation of the roughness irregularities from the mean line over one sampling length (Gadelmawla et al. 2002). As noted above, RMS ( $R_q$ ) is the standard deviation of the distribution of surface heights (Gadelmawla et al. 2002), and is more sensitive than  $R_a$  to large deviations from the mean line. Both  $R_a$  and  $R_q$  are two-dimensional profile measurements. Three-dimensional measurements (across a sample) are potentially more informative as they result from a series of hundreds of 2D profiles (Kumar et al. 2019). Key parameters are RMS deviation ( $S_q$ ) and the sharpness of the asperities ( $S_{ku}$ ) (Zhongxiang et al. 2009).

Although roughness power spectra will provide all information about the asperities of a surface, there may be scenarios where RMS roughness or  $S_q$  can accurately predict maximum frictional adhesion in

geckos (Naylor and Higham Forthcoming 2019), although with considerable variation. As noted above, many parameters of roughness measurements focus on the height or shape of the asperities, but the spacing of the asperities on a surface can also have a significant impact on the ability to adhere (Zhou et al. 2014).

### Adhesion emerges from the sum of the parts

Adhesion is a local issue for an individual seta, but each seta has neighbors and is part of a field that collectively must generate sufficient adhesive force to match the current challenge. The field may be disrupted by, and have to deal with roughness, but this collectivity has been overlooked when adhesive performance of setae has been considered. The vertical pull off force is often represented in images of setal-based adhesion, with the seta essentially vertically disposed relative to the surface. Likewise, studies often visualize how setae insinuate themselves into asperities to make contact. All of this, however, seems to apply only to van der Waals forces and not to frictional adhesion, which is often measured in whole-animal experiments (Irschick et al. 1996; Higham et al. 2017a). For frictional adhesion to occur, the setae have to be lowered into a position essentially parallel to the mean plane of the surface and to the frontal plane of the toe. The length of the setae probing into crevices then becomes moot. We do not understand how setae in different locations can contribute to frictional adhesion at different levels of tilt (which would involve setae adhering beyond the critical release angle). Roughness may just be an exclusionary phenomenon, with adhesive contact only being effective in small islands where the setae can orient effectively. Future work that can visualize setal contact with rough surfaces during frictional adhesion measurements will allow us to connect the dynamics of setal field contact with the forces generated.

### Habitat diversity, roughness, and adhesion: a comparison of plants and rocks

Habitats for lizards are often categorized as being terrestrial, arboreal, or saxicolous (rock dwelling) (see Higham [2019] for discussion). However, this necessarily constrains our view and omits very important information about gecko–habitat interactions. In fact, it is the micro- and nano-scale interactions between a gecko and the surface that likely matter the most, thus requiring micro- and

nano-habitat observations. For example, tree and rock surfaces can be smooth or rough (Fig. 1), compromising the general habitat categorization in attempts to understand the evolution of adhesive function and morphology. Habitat characterization should be on a continuous scale and, at least for geckos, should include a metric that reflects the ability of geckos to cling (e.g., roughness at the appropriate length scale). Along these lines, function should also be quantified along a continuous scale, recognizing that there could be numerous combinations of function and ecology. Below we present a summary of key surface features that are likely important for geckos when holding station or moving.

### Plant surface diversity

When plants colonized terrestrial habitats about 460 mya they faced, compared with their previous aqueous habitat, a rather hostile environment with a desiccating atmosphere and the absence of protection by water against mutagenic UV radiation. To survive under these environmental constraints, an outer protective “shell” was necessary, this being the hydrophobic cuticle which is functionally a continuous extracellular membrane (Riederer and Müller 2006; Koch et al. 2009; Barthlott et al. 2017). In the course of plant evolution, cuticles developed into complex, and sometimes highly specialized, multifunctional interfaces between the inner plant and the environment. One of the major functions of this boundary layer is to serve as a transpiration barrier thereby reducing water loss in the desiccating terrestrial environment, impeding the leaching of ions from the interior of living cells and protecting underlying plant structures. The cuticle is often highly structured and anti-adhesive and/or self-cleaning properties of plant cuticles help reduce contamination and infection by pathogens. Hierarchically structured cuticles are also important for plant–animal interactions and may increase (e.g., in flowers for pollinators) or reduce (e.g., on leaves or stems for avoiding phytophages) attachment and locomotion of animals on plant surfaces. Because the cuticle does not seal the internal plant body entirely from the environment, it thus allows controlled exchange of materials and information for communication between plants, fragrances for communication between plants and animals, and, via stomata, for gas exchange during photosynthesis. The cuticle is thus a communication hub between plants and their biotic and abiotic environment rather than an impenetrable boundary (Koch et al. 2009; Barthlott et al. 2017).

Plants have met the above-mentioned diverse, and sometimes contradictory, functional challenges through the evolution of a plethora of surface structures spanning several orders of length scale, from the sub micrometer range (e.g., wax crystals, cuticular folds) to several millimeters or even centimeters (e.g., multicellular hairs) (Barthlott and Ehler 1977; Koch et al. 2008, 2009; Barthlott et al. 2017). These structures are often combined and form scale-transgressing complex hierarchical surface patterns. Such structures may influence the ability of various animals to attach to plant surfaces and safely walk on them. In the following summary we concentrate on epidermal and cuticular structures because, for nearly all vascular land plant organs (including leaves, petals, fruits), the primary epidermis with its cuticular cover represents a multifunctional interface with the environment. In the context of animal attachment to plants the only important tissue without cuticle is the bark of shrubs and trees, but this may also exhibit complex hierarchical macro- and micro-structuring. At the greatest length scale of the epidermis and cuticle the surface structures include multicellular and unicellular trichomes which may be secretory glands or non-secretory multicellular hairs. Some of the glands may secrete exudates (farina—chemically different from waxes) and may additionally structure the plant's surface. These trichomes may be unbranched or possess a more complex (branched) morphology. Some hairs possess apical structures expressed as barbed hooks or lobed shield-like structures that lie flat on the plant surface. Unicellular hairs are extreme expressions (more than seven times longer than wide) of epidermal cells. The curvature of the outer (periclinal) wall of the epidermal cells markedly influences the surface roughness at the next smaller linear (tenths of micrometer) scale. Usually one of three basic types of curvature characterizes outer epidermal cell walls: flat (tabular), curved to the outside (convex), and curved to the inside (concave), the latter being relatively rare. In addition to these basic forms, specific localized regions of the outer epidermal wall may bulge out or be sunken. In the case of convex excrescences, all transitional forms from slightly convex to hemispherical and papilla-like to the extremal form of unicellular hairs exist.

At the next smaller linear scale (low micrometer to sub-micrometer range) structuring is most often the product of cuticular folding and the often highly sculptured wax layer atop the cuticle. Cuticular folds result from either from the folding of the underlying periclinal cell wall, the presence of sub-cuticular minerals arranged on top of the periclinal cell wall,

or by the folding of the cuticle itself on top of a smooth cell wall. The cuticular folds may be regular or irregular and vary in the height, width, and spacing of the individual folds. They may cover the entire periclinal cell surface or only parts of it, and they often change in shape and size during ontogeny of a plant organ.

Tests of walking-frictional forces exerted by insects on plant surfaces reveal that cuticular folds may either increase or decrease attachment forces (Prüm et al. 2011), and represent an important structural aspect in regard to animals that rely on microscopic setae for attachment. Epicuticular waxes cover (with a few exceptions) the epidermal cells of aboveground primary tissues of all terrestrial plants. They not only contribute to the surface structuring of epidermal cells, but also represent the cuticle's main transport barrier. They can cover the periclinal cell walls as a smooth layer of varying thickness (ranging from a few wax molecules to several micrometers thick). On the wax layer in some plant species epicuticular waxes form complex 3D structures that can range in size from several tenths of micrometer to over 100  $\mu\text{m}$ . They consist of various wax types and exist in a large variety of shapes and orientations and may be arranged in clusters, special patterns (e.g., around stomata), or randomly.

To understand and assess the influence of the often hierarchically combined plant surface structures on adhesion and movement of animals comparative quantitative analyses of the plant surfaces are a prerequisite. To this end a combination of different optical methods including Scanning-Electron-Microscopy, Laser-Scanning-Microscopy, and Atomic-Force-Microscopy are needed. Recent studies (Kumar et al. 2019) showed that Laser-Scanning-Microscopy in combination with appropriate analytical software provides a powerful tool for (semi-)quantitatively describing surface structures including different length scales (Figs. 3 and 4). Additionally, new replication techniques, allowing for the production of translucent and very precise surface replicas (Kumar et al. 2018), may contribute not only to a better ability to quantify complex plant surface structures, but also to the measurement of the real adhesion area available to animal feet on these artificial surfaces, and for correlating them with simultaneously measured adhesion and frictional forces.

### Plant–animal interactions, with insights gleaned from studies of insects and arachnids

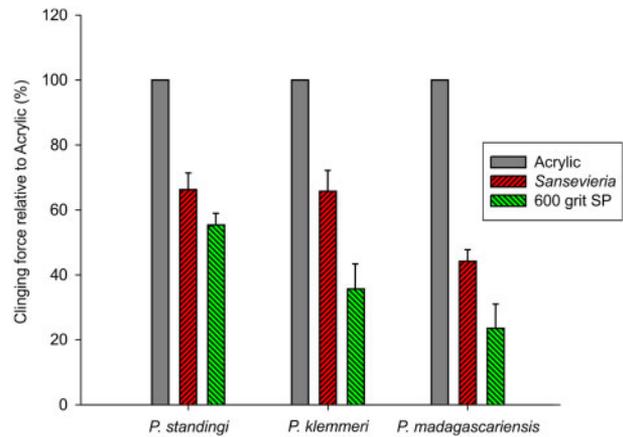
Before making predictions about gecko adhesion, it is important to take account of studies that have examined adhesion and traction forces of insects

with hairy pads. The roughness hypothesis, in which a reduction in the real contact area between the attachment device and the rough substrate is responsible for the reduction in attachment ability, has been examined on several occasions (Prüm et al. 2012). Both plant cell shape (tabular, convex, or papillate) and superimposed microstructures (wax crystals or cuticular folds—see above) have impacts on insect attachment. For example, Colorado potato beetles (*Leptinotarsa decemlineata*) exhibit a strong reduction in traction forces on plant surfaces with medium-sized cuticular folds (*Hevea brasiliensis*, adaxial leaf surface), large cuticular folds (*H. brasiliensis*, abaxial leaf surface), and hierarchical surfaces with cuticular folds (*Litchi chinensis*) (Prüm et al. 2011, 2013).

It is not uncommon for animals bearing hair-like structures on their adhesive apparatus to experience a drop in adhesion or traction force on surfaces with relatively small asperities, and then to subsequently recover on surfaces with relatively larger asperities (Wolff and Gorb 2012; Salerno et al. 2017). For example, southern green stink bugs (*Nezara viridula*) exhibit stronger attachment on surfaces up to a roughness of  $R_a = 4.04 \mu\text{m}$  than on surfaces with very fine asperities ( $R_a = 0.80 \mu\text{m}$ ) (Salerno et al. 2017). In this study and others, the lower force is attributed to the reduction of contact area between the small surface asperities and the size and shape of the fibrillar tips. In other words, low values of roughness can pose problems for animals given that the size of the asperities closely matches the size of the tips, with larger asperities, or increased roughness, providing more contact area for the tips. This is an indicator that the length scale examined should be relevant to the animal and surface when studying roughness.

### Gecko–plant interactions

Many geckos will perch on leaves (Fig. 1), often to sleep (Avilla-Pires 1995). However, plant surfaces are used by some gecko groups routinely during locomotion. This can include tree trunks, leaves, and the surfaces of fruits, or flowers. Thus, the surfaces of plants have likely been critical in driving the evolution of, and molding the function of, the gecko adhesive apparatus. Indeed, some geckos (especially those of the genus *Phelsuma*) exhibit mutualistic relationships with flowering species by consuming their nectar and acting as pollinators (Olesen and Valido 2003; Hansen et al. 2007; Bègue et al. 2014). Therefore, there is potential for coevolution between geckos and plants in the context of feeding and reproduction, but whether this translates into



**Fig. 5** Clinging force (frictional adhesion) of three species of *Phelsuma* on three different surfaces (relative to acrylic). Acrylic is the smoothest, followed by *Sansevieria* and 600-grit sandpaper (roughest). All species exhibited a decline of clinging force with increasing roughness. Standard error bars are shown. Details of the force measurements are found in Higham et al. (2017a).

the evolution of plant surfaces that facilitate gecko adhesion is currently unknown.

We examined the ability of three species of *Phelsuma* to cling to smooth acrylic, a leaf of the succulent *Sansevieria* ( $S_q = 1.67 \mu\text{m}$ ) and, to mimic a rocky surface, 600-grit sandpaper ( $S_q = 4.85 \mu\text{m}$ ; Fig. 4). The methods followed those of Higham et al. (2017a). Relative to acrylic, all three species exhibited a large drop in performance (at least 30%) on the *Sansevieria*, and another drop on the sandpaper (Fig. 5). From this limited sample it is evident that even a “smooth” leaf has asperities that can result in a drop in adhesive ability. Therefore, categorizing surfaces as “smooth” without thorough investigation is problematic.

Naylor and Higham (Forthcoming 2019) assessed how the turnip-tailed gecko (*Thecadactylus rapicauda*) adheres to both natural plant surfaces and a series of artificial surfaces. For plants, only smooth and “hairy” leaves were compared, with the latter being covered by fairly long (up to 1 mm) trichomes. Indeed, frictional adhesive performance was significantly lower on the rough “hairy” leaf ( $S_q = 94.1 \mu\text{m}$ ) compared with the smooth leaf ( $S_q = 6.4 \mu\text{m}$ ). Therefore, for those geckos that perch on leaf surfaces for extended periods of time, or for those small geckos that traverse leaves on a regular basis, leaf microstructure could have a profound influence on performance and survival. This warrants a rigorous investigation of the microtopography of leaves exploited by geckos in nature. For smaller geckos on large leaves, different parts of a leaf could be preferentially used during locomotion. For example, some *Phelsuma* species (e.g., *P. sundbergi*) occupying

large trees (e.g., *Lodoicea maldivica*) preferentially move on petioles, the trunk, or inflorescences (Noble et al. 2011).

### Rocky surface diversity

Metamorphic rocks vary dramatically in their composition and morphology, ranging from very large crystals to very fine asperities (Pedernana et al. 2017). Even a single type of rock, such as quartzite, contains accessory minerals that also vary in composition and shape (Pedernana et al. 2017). Varying amounts of accessory minerals can actually be used to differentiate quartzite varieties, and these will impact the microtopography of the rock surface. However, metamorphic rocks typically exhibit an equigranular texture, a mosaic-tile pattern of interlocking equidimensional mineral grains, as a result of the pressure–temperature environment in which they formed (Dolgoff 1996). This represents a fairly uniform texture and a non-layered appearance (marbles and quartzites). Therefore, metamorphic rocks may generally be more amenable to adhesive contact.

Sedimentary rocks, including sandstones, limestone, gypsum, and conglomerate, among others, vary dramatically in structure as a result of numerous processes. The particles within sedimentary rocks vary in their shape, including sphericity and roundness, and these likely have a large impact on how a gecko might interact with the surface. Rounded particles may provide a larger surface area with which the setal fields can interact, but spacing will likely play a major role as well. Below we present a discussion of gecko morphology in relation to sandstone surfaces in Namibia.

The roughness of a rock surface will also depend on the degree of weathering, including chemical, physical, and biological processes (McCarroll and Nesje 1996). In fact, weathering typically increases roughness, and the degree of weathering is often quantified using the degree of roughness. Weathering can cause surface pitting and differential relief due to crystals, fossils, grains, or veins. Coastal weathering of limestone is a great example. Close to sea level, abrasion is the primary process of weathering, but lichen colonization and salt weathering become more important with increasing height (McCarroll and Nesje 1996). As a consequence, limestone roughness increases with increasing distance above sea level.

### Gecko–rock interactions

In a series of studies (Russell and Johnson 2007, 2014; Russell et al. 2007; Johnson and Russell 2009;

Johnson et al. 2009) the characteristics of substrata routinely used by species of the genus *Rhoptropus* in Namibia were documented and their relationship to the configuration of entire setal fields assessed. *Rhoptropus* was selected for study because it is diurnal (and therefore relatively easily observed in the field), rupicolous, and lacks tractively-functional claws (meaning that substratum contact relies solely on seta-based attachment). Dimensional features of these naturally-occurring substrata (Russell and Johnson 2007, 2014; Johnson and Russell 2009) were compared with those of smooth (Hiller 1968; Irshick et al. 1996; Autumn et al. 2000; Peressadko and Gorb 2004), microscopically rough (Campolo et al. 2003; Persson 2003; Persson and Gorb 2003), and visibly rough (Vanhooydonck et al. 2005) substrata previously used to assess adhesive, clinging, and locomotor performance of geckos.

Pertinent attributes of *Rhoptropus* (snout–vent length, body mass, digit depth, and setal length, diameter, density at selected locations within the setal field), their associated rocky substrata, and previously-employed artificial substrata (attained via 3D imaging and the construction of digital elevation models) were recorded and used to calculate the proportion of the surface able to be contacted by the setae. Employing available force generation estimates for individual gecko setae (Autumn et al. 2000; Autumn 2006), and the setal data acquired for *Rhoptropus*, the total potential adhesive force attainable by all 20 digits was calculated. Using the dimensions of the toe pads and the length of the setae, the amount of surface area accessible to setal attachment for all surfaces was assessed. The smooth and microscopically rough artificial surfaces showed only a relatively small degree of irregularity and were consistent with most of the setae being able to participate in adhesive and shear force generation at the scale of entire toe pads. Contrastingly, the rocky surfaces were found to be not simply rough but rather irregular and undulant, with asperity depths far exceeding the lengths of even the longest setae and with peaks forming localized, patchy points of potential contact (Russell and Johnson 2007, 2014). Calculations revealed that such undulance greatly diminishes the possibilities for setae to make appropriate contact with the surface to effect adhesion, with only small patches across the length and breadth of the toe pad being capable of being involved in this manner on any given footfall. Setal fields, and the toe pads they are carried on, have limited ability to comply with surfaces as undulant as those typified by the rocks on which these species live (Russell and Johnson 2007, 2014). The more

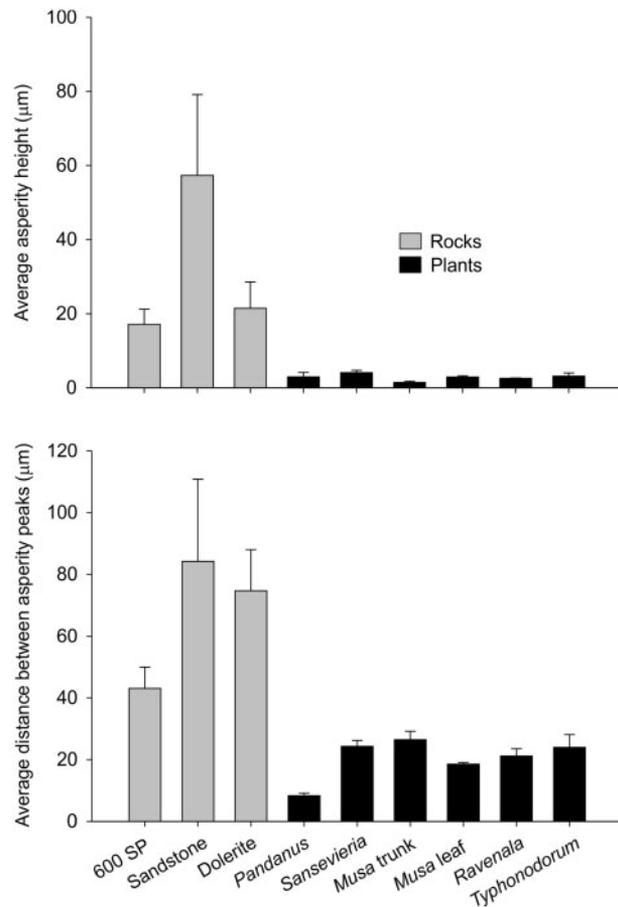
undulant the surface the greater the proportion of exclusionary area (Russell and Johnson 2007).

These findings, like those for *Thecadactylus* landing on leaves (see above), permitted contextualization of the enormous safety margin estimates for total adhesive capacity that have been calculated for geckos (Irschick et al. 1996; Autumn et al. 2000; Autumn 2006). The restriction of potential attachment sites to small patches of the toe pads of *Rhoptropus* on their natural substrata resulted in a reduction of the calculated safety factors by four orders of magnitude. All 20 digits combined for a safety factor of about 10, and a single foot (which may momentarily have to support the whole animal during fast locomotion) had a safety factor of about 2.5 (Russell and Johnson 2007, 2014; Johnson and Russell 2009). The massive total adhesive potential may be regarded as a means of assuring adequate, but patchy, adhesive contact on these naturally-occurring, highly undulant substrata. Such potential localization of adhesive contact may thus be related to the very fine subdivision of gecko setal tips (Arzt et al. 2003), with these highly deformable and compliant structures enhancing the potential for surface contact in localized areas (Campolo et al. 2003; Persson 2003; Spolenak et al. 2005). The entire setal fields are large in relation to the pertinent dimensions (from an adhesive contact perspective) of the terrain traversed, and can conform to small, localized zones but cannot mold to the entire surface (Russell and Johnson 2007).

Geckos that occupy different types of rocky habitats also exhibit differences in their setal morphology. In a study of *Rhoptropus afer* in Namibia, Collins et al. (2015) found that those individuals occupying a relatively horizontal habitat comprised of gravel plains exhibited significantly reduced toe pad area compared with those habitats (e.g., granite outcrops) that were rockier and had more inclined surfaces. Given that these differences were intraspecific, we expect to find considerable differences among species that occupy different types of habitats (different rock and tree types) and also habitats that impose different demands (are more or less inclined).

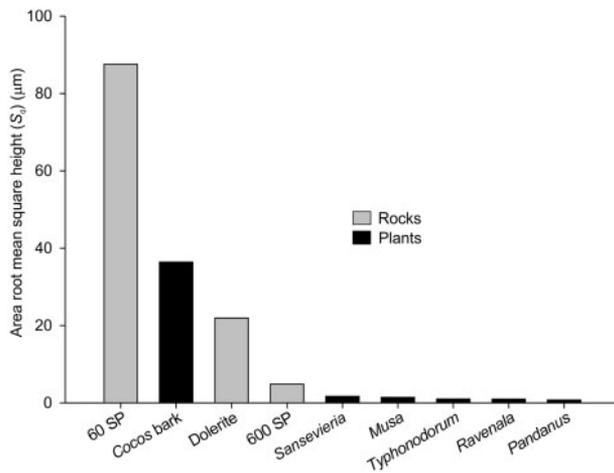
### Differences in adhesion between rocks and plants

What expectations do we have for geckos living on rocks versus plants? Using a confocal laser-scanning microscope (CLSM; LEXT OLS4000, Olympus Corporation, Japan), we analyzed the surface topography of a number of surfaces, including a variety of plants (e.g., Fig. 3), rock-like (sandpaper, Fig. 4), and



**Fig. 6** Average asperity height (top) and spacing (bottom) of a number of rock (and rock-like) (gray) and plant surfaces (black). These were measured from line profiles, as shown in Figs. 3 and 4. The data for sandstone are from Russell and Johnson (2014). Note that the rocky surfaces have higher peaks and greater spacing between asperities than do the plant surfaces.

rocky surfaces. Samples were examined at 20× magnification, and three-dimensional visualization of the surfaces was performed in MountainsMap Premium 7.2 (Digital Surf, France). Using multiple single line profiles, we quantified the average height of the asperities (trough to peak) and the distance between individual peaks. Based on a very limited analysis of height and spacing between asperities (Fig. 6), an interesting pattern emerges. On the one hand, asperities on rocks are much higher, but on the other hand the spacing between the asperities is much greater (Fig. 6). Based on a separate analysis of area roughness ( $S_q$ ), we found that coconut palm (*Cocos*) bark is considerably rougher than the leaves of a number of plant species, and also has the potential to be much rougher than rocky surfaces (Fig. 7). In previous work on cockroaches, increased pillar density of fabricated surfaces limited contact between the pads and the asperities (Zhou et al. 2014). As spacing was increased, full contact was



**Fig. 7** Area roughness of a rock surface (dolerite), two sandpaper grits (60 and 600), and a number of plant surfaces (black). These were obtained in MountainsMap Premium 7.2. Note that plant surfaces (bark) have the potential to be very rough, even when compared with rocks.

made and this was accompanied by a large increase in shear force (Zhou et al. 2014). This mainly applies to rocks and the bark of tree trunks, which both have higher peaks but lower asperity density. However, some plant structures, such as long trichomes, have the ability to disrupt the adhesive system and prevent attachment (Naylor and Higham Forthcoming 2019). For geckos, much more work is needed to determine how the amplitude, density, and shape of asperities influence the ability to adhere.

### Stochasticity and surface topography

Leaf surfaces, unlike rock surfaces, often have a predictable and systematic arrangement of asperities (Prüm et al. 2013; Russell and Johnson 2014; Fig. 3). Figures 3 and 4 show the leaf of a banana and 600-grit sandpaper, respectively, with the latter often being used to mimic a rocky surface in studies of gecko locomotion (Russell and Higham 2009; Higham and Russell 2010; Fuller et al. 2011). Additional images of rocky surfaces can be found in Russell and Johnson (2014). How this might be perceived by a gecko, or if there are morphological/functional correlates of these patterns, is not currently understood. However, one might expect the adhesive strength (on a controlled surface) to be higher for those living on rocks given that they could encounter a situation with very little available surface, whereas a leaf surface is somewhat reliable in its topography. That said, where a gecko is found in nature (at a single point in time) does not necessarily reflect how it uses its habitat. Thus, geckos found

on leaves may encounter a number of other substrates at other times that display an equal amount of unpredictability as a rock surface. Overall, the length, width, branching pattern, and compliance of the setae, along with the shape of the contact point, are likely key in determining how geckos will perform on specific substrates (Spolenak et al. 2005; Collins et al. 2015).

## Observing geckos in nature and exploring habitat selection

### Skewed observations of diurnal geckos

Field observations are critical for understanding gecko adhesion and allow insight into the surfaces employed and, therefore, the challenges that face the adhesive system. However, geckos are ancestrally nocturnal (Gamble et al. 2015; Schmitz and Higham 2018) and the majority of species are active at night. However, several transitions to diurnality have occurred, allowing easier observation of habitat use. It is not surprising that much of what is known about gecko habitat use is restricted to diurnal species from genera such as *Phelsuma* (Harmon et al. 2007; Noble et al. 2011) and *Rhoptropus* (Higham and Russell 2010; Collins et al. 2015), both of which also lack tractive claws. In comparison, relatively few studies have focused on nocturnal geckos (Lisičić et al. 2012; Loos et al. 2012). These observations have detailed microhabitat use by different species, which opens the door to a variety of studies that could link form, function, and ecology. However, we still know strikingly little about how geckos use surfaces in nature, making this one of the grand challenges facing adhesion research as it relates to geckos.

### Utility of enclosure experiments

A powerful tool for experimentally addressing hypotheses regarding gecko habitat use is large-scale experimental enclosures. The major advantages of enclosures are that factors impacting habitat use, including substrate availability, species composition, and lizard density, can be controlled precisely. This level of control allows for replicated comparisons that minimize spatial heterogeneity across experimental units to a degree not achievable when conducting field observations across habitat patches, and allows separation of variables that are often confounded in the field. For example, average perch diameter and degree of shading are often correlated in the field because the largest diameter perches are tree trunks that support shade-creating canopies. In an enclosure, this conflation of perch diameter and

thermal microhabitat can be broken by adding shade cloth to regions with narrow perches, thinning canopy from trees, or providing large diameter perches without canopies, such as posts. While such manipulations could also be done in the field, the starting substrate would differ between patches. In an enclosure, the physical habitat can be created to order. Controlling for habitat availability is critical for drawing inferences regarding selectivity or habitat preference. In order to show preference, it must be shown that animals are using habitat non-randomly with respect to habitat availability. The latter can be measured in the field and accounted for in statistical comparisons, but controlling habitat availability initially in enclosures facilitates the posing of very specific questions and their pursuit in replicated experiments.

Another advantage of enclosures is that detailed observations of known individuals can be collected over time, revealing patterns in habitat use as well as behavioral interactions in different contexts that would be difficult to observe in the field. Wright et al. (in preparation) used enclosures to study competitive interactions between day geckoes (*Phelsuma*) and *Anolis* lizards (all of which are introduced species in Hawai'i) that vary in clinging ability on different substrates. Enclosures were planted identically in an agricultural field with planned availabilities of both smooth and rough perch substrates (Fig. 8A). Lizards were individually marked (Figs. 1B and 8B), and the accessibility of the enclosures allowed for repeated observations of habitat use and behavior. This allowed Wright et al. (in preparation) to document the preferential use of substrate types in association with laboratory measurements of adhesive performance, and shifts in substrate use in the presence of competitors. Rare occurrences such as predation by birds and interspecific displays that were not documented in field observations were observed in the enclosures. In addition, the enclosures allowed for the creation of species combinations that are now rare in the field but critical for determining whether competitive displacement has already occurred in this system. In this case, the relationship between habitat use, substrate availability, and competition could not be tested in the field as these species interactions are already playing out across the landscape.

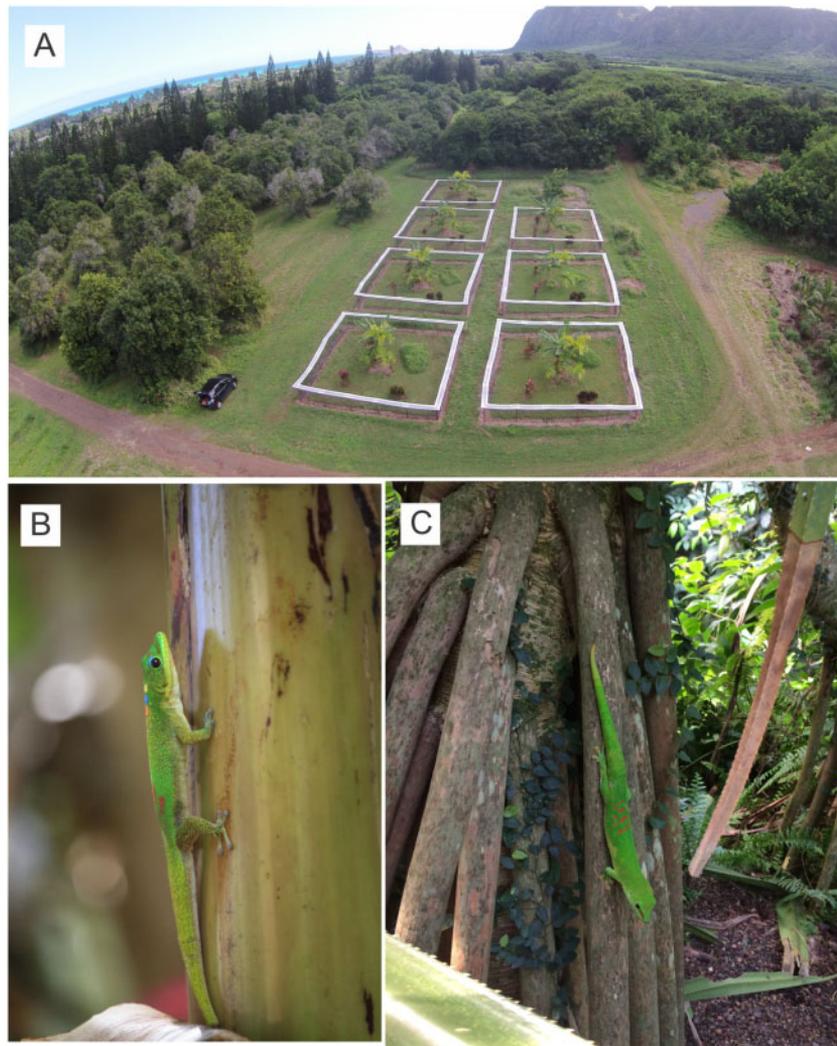
The major drawback to the use of enclosures is the risk of cage effects. These can be minimized by making enclosures as realistic as possible within study constraints by basing design elements, such as habitat availability and lizard density, on field estimates. The generality of inferences from

enclosure studies can be assessed by combining controlled enclosure experiments with field observations and laboratory measurements of performance. For description of a well-used enclosure design that retains many features of natural habitats, such as ambient prey availability, see Pacala et al. (1983).

Going beyond replicated enclosure design, there are options for studying geckos in very large artificial enclosures that attempt to recreate the natural habitat. An excellent example of this is the Masoala Rainforest Exhibition at Zoo Zürich, where multiple species of gecko occupy a large (11,000 m<sup>2</sup>) enclosure populated by more than 35,000 native plants from Madagascar and over 40 other vertebrate species (Furrer et al. 2006). These are powerful systems that can be used for tracking individuals over long periods of time. In fact, recent work has followed the movement distances and microhabitat use of *Phelsuma grandis* (Fig. 8C) across 12 areas in the rainforest exhibit (Wanger et al. 2009). The two most common species of plants visited by individual geckos are *Pandanus* sp. (Fig. 8C) and *Ravenala madagascariensis* (Wanger et al. 2009). By understanding how and why geckos use the substrates that they do, we can begin to understand how the adhesive apparatus may be connected with habitat selection.

### Replicating natural surfaces to study gecko adhesion

Once we know what surfaces geckos use in their natural habitat or in enclosure experiments, how do we go about studying them? Replicating plant surfaces is best done by first creating a negative mold from epoxy, and then a positive mold from PDMS (Kumar et al. 2019). However, this technique cannot be employed for rock surfaces given the hardness of both the rock and cured epoxy. Therefore, a PDMS negative and epoxy positive is optimal. In some cases only a PDMS replica can be used, but this is quite effective (Persson et al. 2018). There are several advantages to replicating surfaces (when compared with using natural surfaces), such as avoiding the degradation of living tissue, standardizing the chemistry and compliance across a range of plants or rocks, and even recreating a fossil surface (Kumar et al. 2019). In some cases, material cannot be exported from field locations, making a replica the only option. Beyond this, replicas can be multiplied and used to create trackways for locomotor experiments, thereby providing a platform for investigating the consequences of ecological variation.



**Fig. 8** Example photos from two different kinds of enclosure experiments. **A)** Replicated enclosures set up in Oahu, Hawaii. **B)** An individual *Phelsuma laticauda* in an enclosure from A. **C)** An individual *Phelsuma grandis* on a *Pandanus* sp. in the Mosoala rainforest exhibit at the Zurich Zoo. Photos from A and B are from AW, and C is from TEH.

### The future: interactions between ecomechanics, biomimetics, and evolution

The easiest way to understand how basic research into ecology and function of biological systems can inform material science research and application is to consider how fundamental knowledge is transferred within the field/paradigm of biomimicry (aka biologically inspired design, biomimetics). In biomimicry, knowledge transfer leading to a novel technical solution (e.g., application of the lotus leaf effect for the creation of self-cleaning coatings) usually emphasizes the way in which a biological principle(s) lends itself to a technological solution. Often, this occurs unintentionally at the expense of fully revealing how the process can also advance basic research on the technical side (e.g., material science).

Speck et al. (2017) and Speck and Speck (2008) describe the complementary advancement of knowledge on the biological and technical side as a “heuristic spiral.” Taking gecko adhesion as an example, the “spiral” is evident at many levels of abstraction: The idea that a fibrillar (hairy) surface could be “sticky” has been evident for quite some time, but only recently was it shown that the nanometer-sized spatulate tips of gecko setae are attracted to surfaces by van der Waals forces (Autumn et al. 2000). Autumn et al. (2002)’s experiments pushed the limits of tribological measurement technologies (AFM and SEM); contact mechanics theory (Persson 2003; Persson and Gorb 2003); and materials research, design, and fabrication (Greiner et al. 2009a, 2009b). Beyond the initial discovery of hairy adhesive systems in biology, current gaps in the understanding of how such systems allow organisms

to cope with surfaces that are dirty or rough will not be closed without returning to functional ecological studies that reveal characteristics and parameters of the gecko toe pad systems that are likely tuned to specific aspects of the highly varied environments that the more than 1800 species of geckos inhabit.

At least two areas of inquiry for which both our understanding of the gecko system and the state of the art of our gecko inspired synthetic adhesive are limited relate to the maintenance of functionality where surfaces are rough or dirty. Gecko toe pads are self-cleaning because of two proposed mechanisms: one passive and the other active (Hansen and Autumn 2005; Hu et al. 2012). Interestingly, we have very little information about how and what kind of surface contamination exists or creates problems for geckos on natural substrates, although in at least two cases we know that substrate contamination can affect habitat usage by geckos that rely on toe pads (Cole et al. 2005; Russell and Delaugerre 2017). Commercially-available gecko-inspired adhesives (King et al. 2014) currently exclude mimicking the fibrillar contact surface of skin due to the challenges of replicating the size and geometry of the setae. These adhesives are able to match gecko performance in several ways, but are not self-cleaning. Although the smooth elastomer surface can be washed for repeated use, this is not the same as self-cleaning, which may be an emergent property of the fibrillar geometry and mechanics of toe peeling. It is precisely at this gap in knowledge that more study of the natural surfaces used by free-ranging geckos, combined with further analysis of the potential importance of fibrillar design for self-cleaning, is needed. Data from such studies will allow us to determine the potential value of pushing our current limits in manufacturing technology to capture an aspect of the original design for our synthetics. Moreover, studies of the way in which setae branch could inspire new ways of thinking about creating synthetic mimics that currently limit our approaches, either technologically or economically. We expect, and depend upon, another wave of discovery sourced from renewed attention on ecomorphological analysis to drive hypothesis generation and testing through materials research (Autumn et al. 2014; Niewiarowski et al. 2016).

Geckos obviously play a major role in the development of synthetic bioinspired adhesives. These have come a long way since 2000, but understanding how geckos use natural surfaces has been identified as being key to advancing synthetics (Niewiarowski et al. 2016) for two main reasons. Firstly, geckos are often successful at being able to adhere to rough

surfaces in nature whereas synthetic adhesives often fall short of this capability. By understanding not only how geckos move on these surfaces, but also what micro- and nano-scale adaptations might exist for different surface types, we might be able to apply this information to the development of smart surface adapted synthetics. Secondly, robots that incorporate a fibrillar adhesive system face the difficulty of attaching and detaching their adhesive system. By knowing how geckos modulate their locomotion on different surfaces, we can potentially incorporate such information into the creation of more effective (i.e., faster and more versatile) robots.

### Surface generalists versus specialists, and what we can learn from them

Some species of gecko appear to be substrate generalists, being found on a wide array of surfaces. For example, *Tarentola mauritanica* can be found on artificial surfaces, on the ground, in caves, on rocks, and on trees (Din 2006). Because of this, one might expect it to display a versatile adhesive system that is effective on several different types of surfaces. This might result in a trade-off whereby adhesive strength is not maximized for any single type of surface. In contrast, some species of gecko appear highly restricted in their substrate use. An excellent example of this is *Phelsuma ravenala*, which is a specialist found only on a single species of plant (*R. madagascariensis*) (Raxworthy et al. 2007). In this case, the likelihood that the adhesive system has co-evolved with the plant surface is high, potentially leading to maximizing adhesive strength on one surface but highly reduced performance on others. Exploring the morphological and functional space of both generalists and specialists may unveil novel sources of inspiration for synthetic adhesives.

### On the move! The importance of locomotor biomechanics on different surfaces

Much of what we know about gecko adhesion derives from static experiments, but geckos frequently ambulate over complex terrain. The interaction between the setal fields and the substrate could differ substantially when a gecko must repeatedly peel the toes at the end of stance and make contact when the toes are unfurled onto the substrate at footfall. This can result in the increase of kinetic friction. Dynamic locomotion may involve considerable slippage, whether smooth sliding or stick-slip friction (which occurs when the static friction force is greater than the kinetic friction force). A recent study found that while stick-slip friction disappears

as shear velocity of a synthetic gecko adhesive mimic increases across a smooth silica surface, stick-slip was always present when pulled across a rough surface (Das et al. 2015). Thus, there could be significant consequences for geckos as they actively run across surfaces of varying roughness, and geckos may actively modulate their kinematics to account for this. By varying the velocity of locomotion, kinetic friction can be modulated.

Geckos not only move across level surfaces, but can move up, down, and across surfaces of varying inclines and perch diameters (Birn-Jeffery and Higham 2014, 2016; Zhuang and Higham 2016). Maintaining effective traction while employing a directional adhesive system is a challenge that geckos overcome, in part, by the spread of their digits and the modulation of their limb segments and digit orientation to maximize shear force generation when holding station (Russell and Oetelaar 2016) and while moving (Birn-Jeffery and Higham 2014). Incorporating information from all four limbs, and all toes, will provide an important holistic view of gecko adhesion on rough surfaces. If one foot, toe, or even an area of a toepad, fails to make contact with a patch of substrate, it is possible that other parts can compensate.

The process of unfurling the toes to engage the adhesive system with the substrate is dynamic and occurs after initial contact with the substrate. Therefore, for each foot there is a portion of time during the locomotor cycle in which there is no contact between the adhesive apparatus and the surface. At the end of the stance phase, the digits are hyperextended (Russell and Higham 2009), again resulting in a short period of time without adhesive contact. While in contact, and with the body still moving forward, posterior motion of the foot (i.e., slipping) can occur (T. E. Higham, personal observation), which will necessitate more complex models of friction.

### How material science research can inform ecological and functional research

As biologists, we often think of how biological systems can inspire the formation of synthetic material, the design of a robot, or an application for industry. However, material science research can inform and inspire biological research in a number of ways. For example, by creating surfaces that are beyond what is observed in nature, we can build on our understanding of the limits of the adhesive system. Similarly, synthetic fibrillar adhesives can be used to test

options that were not explored during gecko evolution. Empty spaces within an adaptive landscape provide a window into evolutionary and mechanical constraints. Finally, synthetic adhesives that mimic those of a specific species of gecko can be taken into nature and tested on a variety of natural surfaces, thereby exploring how a particular species might perform in a variety of habitats. This could be an avenue for exploring questions related to convergent evolution. Ultimately, the advancement of research on gecko adhesion will be facilitated by reciprocal illumination from disparate scientific fields.

### Conclusion

Revisiting our initial goals, ecology should be incorporated into gecko adhesion research in order to gain a better understanding of how adhesion may have originated, why it is seemingly overbuilt, and to generally understand the ecology and diversity of geckos. Asperity size, spacing, and shape are the likely drivers of adhesive performance, although we still know very little about how setal fields interact with surfaces when employing frictional adhesion. Rock surfaces are shaped by numerous processes, including weathering, formational composition, and temperature–pressure history. Plant surfaces are very diverse, exhibiting cuticular folds, trichomes (which can be glandular, hooked, or branched), and wax crystals. Additionally, the curvature of the epidermis may have impacts on adhesion. There is potential for co-evolution between geckos and plants, especially when mutualistic interactions occur (as in *Phelsuma*). Finally, ecomechanical research can inform biomimetics through a deeper understanding of how geckos move effectively over rough and dirty surfaces. The next decade or two will unearth numerous exciting advancements that capitalize on an interdisciplinary approach.

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