# Mechanics reveals the role of peristome geometry in prey capture in carnivorous pitcher plants (*Nepenthes*)

Derek E. Moulton<sup>1,†</sup>, Hadrien Oliveri<sup>1</sup>, Alain Goriely<sup>1</sup>, and Chris Thorogood<sup>2,†</sup>

<sup>1</sup>Mathematical Institute, University of Oxford, Oxford OX2 6GG, United Kingdom; <sup>2</sup>University of Oxford Botanic Garden, Oxford OX1 4AZ, United Kingdom

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Carnivorous pitcher plants (Nepenthes) are a striking example of a 1 natural pitfall trap. The trap's slippery rim, or peristome, plays a 2 critical role in insect capture via an aquaplaning mechanism that is 3 well documented. Whilst the peristome has received significant re-4 search attention, the conspicuous variation in peristome geometry 5 across the genus remains unexplored. We examined the mechanics of prey capture using Nepenthes pitcher plants with divergent peristome geometries. Inspired by living material, we developed a 8 mathematical model that links the peristomes' three-dimensional ge-9 ometries to the physics of prey capture under the laws of Newtonian 10 mechanics. Linking form and function enables us to test hypothe-11 ses related to the function of features such as shape and ornamen-12 tation, orientation in a gravitational field, and the presence of 'teeth', 13 while analysis of the energetic costs and gains of a given geometry 14 provides a means of inferring potential evolutionary pathways. In a 15 separate modeling approach, we show how prey size may correlate 16 with peristome dimensions for optimal capture. Our modeling frame-17 work provides a physical platform to understand how divergence in 18 peristome morphology may have evolved in the genus Nepenthes in 19 response to shifts in prey diversity, availability, and size. 20

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arnivorous plants evolved various forms of leaf-derived 1 traps that attract, capture, retain, kill, and digest animal 2 prey, as a mode of survival in nutrient-poor environments. 3 Nepenthes is a tropical genus of carnivorous pitcher plants 4 that produce specialized pitfall traps. Insects are attracted by 5 lures such as coloration and nectar, and become trapped when 6 they 'aquaplane' off the slippery pitcher rim (peristome), a surface structured with specialized ridges (1, 2), leading them 8 to fall into a vessel of digestive fluid (3). The insects release 9 nitrogen which gives the plants a strong selective advantage in 10 environments where light and water are plentiful, but nutrients 11 are limiting (4). 12

The specialized trapping surfaces of carnivorous Nepenthes 13 pitcher plants are receiving growing interest from biologists 14 15 and engineers because of their strong biomimetic potential (5). For example, the slippery trapping surface of the Nepenthes 16 pitcher has inspired Slippery Liquid-Infused Porous Surfaces 17 (SLIPS) which have exceptional wettability performance (6, 7). 18 Yet despite research focused on the peristome as a key feature 19 in the evolution of the trap, and as a source of inspiration 20 to technologists, little is known about the mechanics of prey 21 capture in *Nepenthes*, or how this varies among species. 22

To date, there are 179 accepted species of *Nepenthes* (POWO, 2022) and they show an astonishing diversity in pitcher morphology. Little is known about the prey trapped by most species in nature. Among the few species in the 26 genus examined, diversity seems to mirror a range of nutrient 27 acquisition strategies linked to habitat characteristics (8). For 28 example, ants are a common form of prey in lowland habitats 29 (9), whereas flying insects are often trapped by plants growing 30 in mountain environments (10). More specifically, research in 31 the last two decades has revealed that divergent pitcher mor-32 phology is linked to nutrient acquisition sources ranging from 33 termites (9), and leaf litter (11), to mammalian feces (12, 13). 34 Most recently, a species was reported from Borneo that pro-35 duces pitchers underground (14). This diversity in pitcher 36 function appears to be the result of an adaptive radiation 37 driven by dietary shifts, analogous to well-known examples in 38 animals, such as the diverse beak shapes of Darwin's finches 39 and the various adaptations of cichlid fish in the African Great 40 Lakes (3). However, only a fraction of the diversity of Ne-41 penthes has been examined, and we know little or nothing of 42 the prey spectrum for most species. 43

The general mechanism by which insects slide off the Ne-44 penthes is well documented. A film of water stabilizes on the 45 superhydrophilic surface (1). The surface is covered by a regu-46 lar, hierarchical microstructure of parallel ridges, or channels 47 (2, 5). These ridges guide prey into the trap in a controlled 48 way through (5). Macroscopic ridges restrict lateral but en-49 hance radial spreading of water, hence creating slippery chutes. 50 Meanwhile, microscopic ridges ensure the watery film between 51 the insects' feet and the peristome remains stable, causing 52 insects to aquaplane (2). These principles seem to be consis-53 tent across multiple species, indicating a common mechanism 54 underlying insect aquaplaning. However, the gross morphology 55

### Significance Statement

Pitcher plants (*Nepenthes*) produce an astonishing array of leaf-derived traps into which prey (typically insects) slide from a rim (the peristome). How prey capture varies across this varied genus is a mystery. We hypothesized that the ability to capture an insect is connected to the peristome geometry and relative size. We demonstrated this connection by examining the physics of prey capture under the laws of Newtonian mechanics. Our analysis suggests that a diversity of peristomes in *Nepenthes* evolved in response to variation in prey capture.

CT introduced the problem. All authors designed the study. DEM developed and analyzed the peristome surface models. HO developed and analyzed the finite-size prey model. All authors contributed to the writing of the manuscript.

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 $<sup>^\</sup>dagger$  To whom correspondence should be addressed. E-mail: derek.moulton@maths.ox.ac.uk, chris.thorogood@obg.ox.ac.uk



Fig. 1. Divergent morphology in the genus Nepenthes shown by (a), the flat peristome of N. jacquelineae; (b-c) the prominent teeth (arrow) of N. hamata, and (d) the conspicuously flared peristome of N. veitchii. Photos (a) and (d) by Domonick Gravine; photos (b-c) by Jeremiah Harris.

of peristomes is conspicuously diverse in size and geometry, 56 ranging from cylindrical rims to highly ornate, fluted, and 57 toothed structures (Fig. 1). This diversity can be linked to 58 ecological niche. For example N. veitchii [Fig. 2(b)] has an 59 unusual life history: the plant clings to trees with the pitchers 60 oriented such that the ventral surface is parallel to the tree 61 surface. Meanwhile species such as N. macrophylla and N. 62 diabolica [Fig. 2(d)] produce pitchers, often half-buried in moss, 63 with conspicuously toothed peristomes. Unfortunately, the 64 prey spectrum of these-like the majority of species-and the 65 function of these structures, are poorly undocumented. Why 66 peristomes are so variable and how their geometry relates to 67 prey capture, remains unknown. 68

Here we present a mathematical framework to link divergent 69 three-dimensional peristome geometries to the physics of prey 70 capture. Linking form and function, we test the hypothesis 71 that shape and ornamentation, orientation in a gravity field, 72 presence of teeth, and peristome size, influence the diversity 73 of prey capture in Nepenthes. 74

#### 1. Mathematical approach 75

Our objective is to develop a mathematical framework linking 76 peristome geometry to prev capture to investigate whether the 77 observed diversity in peristome geometry can be understood in 78 simple physical terms relating to prey-capture functionality. Of 79 the 179 known species, there exists a wide variety in peristome 80 size and morphology. Here we focus on three key geometric 81 features of the peristome: i) the peristome width and presence 82 and degree of peristome *flaring* - broad and often fluted, ii) the 83

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*orientation*, or tilt, of the peristome with respect to gravity, 84 and iii) the presence of surface features such as *ribbing* or in 85 extreme cases, teeth - prominent spine-like, parallel features. 86 Based on these features, we classify Nepenthes peristomes into 87 four categories that could be easily compared, as illustrated 88 in Fig. 2(a)-(d), Base, Flared, Flat, and Toothed: 89

• **Base** peristomes are thin with a roughly  $45^{\circ}$  tilt with respect to the vertical, and inconspicuous ribbing. A 91 paradigm for this type is N. pervillei, a species from the Seychelles, established to be sister to all other species of Nepenthes (15). It is reasonable to assume that other, more ornate patterns of geometry, evolved from this ancestral state.

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- Flared peristomes are similar to the base geometry distally (at the front), but flare out to varying degrees proximally (near the point of attachment to the lid).
- Flat peristomes have a similar geometry to Base, but with 100 a wider rim. These peristomes are distinct from the flared 101 ones in that they are more uniform in width. They are 102 also characterized by a flatter orientation with respect to 103 gravity compared with the other types which are tilted 104 such that the proximal region is lower than the distal 105 portion. 106
- Toothed peristomes also have a similar geometry to Base-107 thin and without flaring-but possess prominent ribs, so 108 large that they are often referred to as 'teeth', protruding 109 from the peristome and projecting into the pitcher interior. 110 Despite their conspicuousness, their function is unknown. 111

The surface characteristics particular to each category may 112 be quantified in terms of 5 basic measures denoted schemati-113 cally in Fig. 2(e)(i): i) the interior peristome length (L); ii) 114 the minimum  $(W_1)$  and maximum  $(W_2)$  peristome widths; iii) 115 the angle of the peristome with respect to gravity  $(\phi)$ ; and 116 iv) the average ribbing height (H). From these, we define the 117 peristome relative width  $W_2/L$ , the degree of flaring  $W_2/W_1$ , 118 the prominence of ribs/teeth  $H/W_1$ , and the orientation  $\phi$ . In 119 Fig. 2(e)(ii)-(iii) we plot these values for each of the sample 120 species (see SM Section 1C for details on parameter extrac-121 tion), from which the distinctive features of each group are 122 quantitatively apparent. (Peristome curvature is also relevant 123 in prey capture, but is not included as a measure here as it is 124 less practical to define a single meaningful value that can be 125 extracted from an image.) 126

To explore fully the potential functions of the features 127 described above, we must first establish a robust mathematical 128 framework that can describe accurately the diverse geometries 129 involved. In Supplementary Material (SM) Section 1, we have 130 outlined a systematic procedure for creating parameterized 131 mathematical surfaces that model various peristomes. The 132 construction process consists in defining first a space curve 133 defining the basic peristome shape; we then construct explicit 134 cross-sectional shapes at discrete points along the peristome, 135 through which we have fine control over local curvature and 136 features such as flaring; interpolation between these cross-137 sections leads to construction of the full surface. The peristome 138 shape and curvature profile were varied until a reasonable 139 visual match with the chosen specimen was reached. This 140 approach allows us to generate realistic peristome geometries 141 that can be modified easily and continuously as needed as 142



Fig. 2. Variation in peristome geometry and mathematical reconstructions. We categorize peristomes into 4 categories: (a) Base geometry, exemplified by *N. pervillei* (top) and *N. eymae* (bottom); (b) Flared geometry, exemplified by *N. veitchii* (top) and *N. naga* (bottom); (c) Flat geometry, exemplified by *N. macrophylla* (top) and *N. diabolica* (bottom). Mathematical surface reconstructions for each peristome are shown at right for each species. Details on the mathematical construction process are given in SM Section 1. Quantification of surface properties is demonstrated in (e). From the 5 surface measures shown in (e)(i), we define 4 (dimensionless) surface properties: peristome flaring is plotted against relative width in (e)(ii); relative ribbing/teeth height is plotted against orientation angle in (e)(iii) for all sample species and model reproductions. *N. pervillei* photo by Ulrike Bauer; *N. eymae* photo by Sarracenia Northwest; *N. jamban, N. naga, and N. macrophylla* photos by Tom Bennet (tomscarnivores.com); *N. jacquelinae, N. veitchii*, and *N. diabolica* photos by Jeremiah Harris.

shown in Fig. 2. The characteristic measures defined above 143 may also easily be extracted from the mathematical surfaces; 144 these data points are included in Fig. 2(e)(ii)-(iii), showing 145 good proximity with the peristomes being representated. By 146 employing this construction process, we can create a wide 147 range of peristome shapes and configurations, and investigate 148 their properties and functions. For a given peristome type, 149 we have a vector of parameters  $\mathcal{S}$  that defines the peristome 150 surface  $\Sigma \subset \mathbb{R}^3$ . 151

Given a peristome surface  $\Sigma(\mathcal{S})$ , we characterize prev cap-152 ture capabilities by first considering the sliding of a point mass 153 on the surface  $\Sigma$  as a function of surface wetness. Neglecting 154 the deformation of the peristome due to the small mass of 155 the insect, we assume that the peristome remains fixed and 156 rigid. The first question is: Is an insect's position  $\mathbf{p} \in \Sigma$  on 157 the surface stable under the force of gravity? This is a simple 158 geometry problem that involves determining the local peris-159 tome orientation in the gravitational field using the normal 160

vector **n** to  $\Sigma$ , and the coefficient of static friction  $\mu$ .

The effect of increasing wetness is to reduce the stability of 162 most positions. Therefore, our second question is crucial: If a 163 position on the peristome is unstable, will the insect slide into 164 or out of the pitcher? The dynamics of a point mass on the 165 peristome is given by a system of differential equations that 166 can be integrated in time until either the inner or outer edge 167 of the peristome is reached. Points whose trajectory leads 168 to the inside rim of the peristome will be deemed caught by 169 the pitcher, contributing nutrients to the plant, while points 170 whose trajectory leads to the outside rim will fall off the edge, 171 contributing nothing. 172

Details outlining this procedure and our computational approach can be found in SM Section 2. Since we have an explicit surface parameterization, we can easily calculate surface stability and sliding dynamics and divide the surface  $\Sigma$ , for a given friction coefficient, into different non-intersecting regions of total area  $\mathcal{A} = \mathcal{A}_{stable} + \mathcal{A}_{unstable} = \mathcal{A}_{stable} + \mathcal{A}_{in} + \mathcal{A}_{out}$ 

and:

 $\Sigma_{\text{stable}}$ : stable region of area  $\mathcal{A}_{\text{stable}}$ ;  $\Sigma_{\text{in}}$ : unstable region, prey falls in, with area  $\mathcal{A}_{\text{in}}$ ;  $\Sigma_{\text{out}}$ : unstable region, prey falls out, with area  $\mathcal{A}_{\text{out}}$ .

Next, we use the above approach to analyze flaring, orientation, and ribbing features. It is important to highlight the
modeling trade-off: the analysis in these sections is carried out
on detailed and realistic geometries, but using a highly idealized and simplified description of the insect itself as a point
mass. To complement this analysis, we present, in Section 5,
a second model that takes into account the size of the prev.

# 180 2. The benefits of a flared peristome

The pitcher plant species *N. veitchii* [Fig. 2(b)] has a striking peristome, which is broad and oblique. This peristome type is also observed in other species such as *N. nebularum*, *N. hurrelliana*, *N. naga*, and *N. robcantleyei*. However, the prey spectra of these species in their natural habitats remain undocumented, and the evolutionary drivers behind this peristome morphology are still unknown.

To gain insight into the potential benefits of a Flared peristome for prey capture, we first analyze the stability properties of the peristome surface as wetness increases. By examining the peristome geometry and its response to different levels of wetness, we can develop a better understanding of how this structure functions and how it may have evolved to suit the needs of the plant.

In Fig. 3(a), we present the result for our model of a Flared 195 peristome, with each point of the surface colored according to 196 197 the vantage of the insect giving both its stability and dynamic properties: points in the region  $\Sigma_{\text{stable}}$  are green (safe); points 198 in  $\Sigma_{in}$  are labeled red (unsafe), and points in  $\Sigma_{out}$  are labeled 199 black. The different surfaces correspond to differing degrees 200 of 'slipperiness': the friction coefficient, denoted  $\mu$ , decreases 201 following the arrow, corresponding to a more slippery surface. 202 Naturally, as the surface becomes more slippery, a larger 203 area becomes unstable; indeed  $\Sigma_{\text{stable}}$  shrinks to a set of zero 204 area in the limit of zero friction. It is also unsurprising that 205 points on the inner rim, where the surface becomes nearly 206 vertical, are red (the dynamics end with the prev falling in), 207 with this red region  $\Sigma_{in}$  expanding with increasing slipperiness. 208 The black region,  $\Sigma_{out}$ , is "useless" to the plant, as prey located 209 at these points will fall out of the pitcher. It is interesting 210 to note that  $\Sigma_{out}$  remains relatively small until very high 211 slipperiness, and always has a smaller area than  $\Sigma_{in}$ . 212

Nectar glands are located near the inner rim of the peris-213 tome. Therefore, it is in this general direction that prev are 214 likely to be attracted. Further, a recent study (16) presents 215 a capture mechanism in which scout ants are able to walk 216 on the peristome surface without sliding and falling in; these 217 218 scout ants recruit workers, enabling a batch catch and thus greater benefit than if the scout ants had fallen in. In the 219 context of these two points, Flared geometry may be adaptive 220 for capturing walking prev such as ants. At low slipperiness, 221 there are few black regions; thus the surface geometry provides 222 a safe platform for scout ants to locate nectar, and subsequent 223 worker ants to follow pheromone trails to the red region. As 224 slipperiness increases, stable green 'corridors' enable insects to 225 walk from the outer edge of the peristome to the red region, as 226



**Fig. 3.** The impact of flaring on prey-capture. (a) Stability and capture properties of a Flared peristome as friction coefficient  $\mu$  is decreased. Green points are stable, red points slide into the pitcher, and black points slide out. Stability 'corridors' – stable paths from the edge of the peristome to the unstable inner rim – are highlighted with blue lines and arrows. (b), (c): net energy gain  $\Delta E$  plotted for peristome flaring,  $W_2/W_1$ , and for different values of energy benefit parameter  $c_g$ , for normal flaring (b) and lower rim flaring (c). The point of maximum  $\Delta E$  is denoted with a star. In (b), measured flaring values (given as an approximate range) for *N. veitchii* and *N. pervillei* are indicated. Right: the peristome geometry at indicated values of  $\alpha$ , with fall-in and fall-out points shown in red and black, respectively.

highlighted by blue arrows in Fig. 3(a). Owing to the climbing habit of *N. veitchii*, the proximal portion of the peristome often touches the vertical axis of the supporting tree. Here the flared peristome may act as a corridor to the pitfall trap – a form of shuttle for insects crawling up and down the tree. 231

Energy considerations A fundamental trade-off exists in car-232 nivorous plants: leaves are modified into traps at the expense 233 of photosynthetic efficiency because the traits of an effective 234 insect trap are incompatible with those of an efficient light 235 trap (4). Our analysis of Flared peristomes indicates a similar 236 trade-off between prey capture and cost associated with the 237 production of a peristome. The peristome contributes little to 238 photosynthesis, and is costly to construct (17), suggesting a 239 strong selective advantage to such a structure in a nutrient-240 stressed environment. Quantifying such trade-offs between 241 peristome investment and prey capture with empirical data 242 is challenging, not least since the identity of prey in nature is 243 unknown for most species. Nevertheless, we gain insight into 244 this problem by using a modeling approach in which we as-245 sume that the energetic benefit, denoted  $E_{\rm gain},$  is an increasing 246 function of the capture surface area; that is 247

$$E_{\text{gain}} = g(\mathcal{A}_{\text{in}}),$$
 [1] 248

where g is a monotonically increasing function. This models the assumption that the benefit increases with the number of prey caught and that the number of prey caught increases with the area of peristome from which prey fall. The situation may be different for flying versus walking prey, given that flying prey can land anywhere on the surface while walking prey can only access stable portions as a starting point. Though given how little is known of the prey spectra of most species, we leave more detailed modeling for future work. Since  $A_{in}$ depends on the friction coefficient  $\mu$ , we compute  $A_{in}$  in the case of a perfectly wetted surface ( $\mu = 0$ ), for simplicity. We model the energetic cost as an increasing function of the total peristome area, that is

$$E_{\text{cost}} = f(\mathcal{A}) = f(\mathcal{A}_{\text{in}} + \mathcal{A}_{\text{out}}), \qquad [2]$$

the latter equality reflecting the fact that the stable area shrinks to zero when  $\mu \rightarrow 0$ .

265 We can then define the net energy

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$$\Delta E := E_{\text{gain}} - E_{\text{cost}} = g(\mathcal{A}_{\text{in}}) - f(\mathcal{A}).$$
 [3]

We want to express  $\Delta E$  as a function of a given peristome 267 feature that may be varied through natural developmental 268 mechanisms. Then, through evolution by natural selection, 269 the feature may be expected to converge to the point where 270  $\Delta E$  is maximal, or at least near to it (as other factors may 271 impact the total evolutionary fitness). If changing a given 272 feature decreases  $\Delta E$ , we do not expect to see such changes 273 in nature. Of course, it will depend on the specific form 274 of the functions f and g. Here we consider a generic form 275  $g(x) = c_g x^{\beta_g}, f(x) = c_c x^{\beta_c}$ , where the constants  $c_g$  and  $c_c$ 276 characterize the energetic gain and cost, respectively, i.e. the 277 impact of increased capture area and total area, while the 278 exponents  $\beta_q$  and  $\beta_c$  characterize possible non-linearity in the 279 pathway between areas and energy. 280

We now examine flaring under this framework. Our con-281 struction method enables us to continuously vary the degree 282 of flaring, from thin (as in **Base**) to a widely flared peristome, 283 or even beyond what is observed in nature. Therefore, we 284 express  $\Delta E$  as a continuous function of the flaring parameter 285  $W_2/W_1$  where  $W_2/W_1$  ranges from 1.0 (unflared, similar to 286 N. pervillei) to 9.0 (more flared than what we have measured 287 on N. veitchii) – for details on continuously varying flaring, 288 see SM Section 1. For a given  $W_2/W_1$ , we seed the peristome 289 with a uniform distribution of point masses, integrate forward 290 the dynamic trajectories, and compute the capture (and miss) 291 areas as fractions of total area based on the number of tra-292 jectories leading to the inner (and outer) rim (details in SM 293 Section 2). In Fig. 3(b), we plot  $\Delta E$  over a range of values of 294  $W_2/W_1$  for varying choices of  $c_g$ , where we have fixed without 295 loss of generality  $c_c = 1$ , and with other parameters taken 296 for simplicity to be  $\beta_c = \beta_g = 1$  (see also SM section 2D 297 for an analysis of how varying these parameters impacts the 298 net energy). For each choice of  $W_2/W_1$  the maximum of  $\Delta E$ 299 is denoted with a star. For low values of  $c_q$ ,  $\Delta E$  decreases 300 monotonically with  $W_2/W_1$ . Here, the benefit from increased 301 prev capture is relatively low: the cost of increased total area 302 outweighs the gain from increased capture area; for a species 303 with these parameters, it would not be energetically favorable 304 to increase flaring. For an increased  $c_g$ , however,  $\Delta E$  exhibits 305 non-monotonic behavior, and indeed with an interior maxi-306 mum, the degree of flaring to which our model would predict 307 selection pressures will drive the feature. 308

One great advantage of modeling is that it allows us to investigate features that are not found in nature. For instance, in Fig. 3(c), we repeated the same analysis, but with flaring along the bottom rim of the peristome. Such peristome geometries are not observed in nature, and our energy model demonstrates why this might be the case: the increased area at the bottom rim does not contribute to prey capture, as prey located there will fall out of the pitcher when slippery. Thus, increasing flaring in this manner does not result in a net benefit. This is evidenced by the fact that  $\Delta E$  decreases as flaring increases for all the tested values of  $c_g$ , rendering it a non-adaptive feature. 320

### 3. Peristome orientation

Next we consider the orientation of the peristome with respect to the vertical. Peristome orientation varies conspicuously across the genus from near-horizontal, for example in N. jamban and N. jacquelinae [Fig. 2(b)], to an orientation of ca. 45°, for example N. veitchii and N. naga [Fig. 2(c)].

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To determine the relevance of peristome orientation to 327 prey capture, we have varied this angle, defined as  $\phi$  in our 328 construction (see SM Section 1), from being flat ( $\phi = 0$ ) to 329 vertical ( $\phi = 90^{\circ}$ ), while also varying the friction coefficient  $\mu$ . 330 Considering again the Flared peristome model, Fig. 4(a) shows 331 how the regions  $\Sigma_{\text{stable}}$  (green),  $\Sigma_{\text{in}}$  (red), and  $\Sigma_{\text{out}}$  (black) 332 vary both with tilt and friction coefficient. This simulation 333 shows that tilt strongly impacts stability: the flat peristome 334 has most points stable, while the highly tilted peristome has 335 most points unstable. Also of note is that at large and small 336 tilts (top and bottom rows), changing  $\mu$  has almost no impact, 337 while it has a strong impact at the intermediate tilt  $\phi =$ 338  $45^{\circ}$ . This is particularly relevant in the context of scout ants 339 recruiting large numbers of ants to walk on a surface, and 340 the need for a stable corridor from the edge of the peristome 341 to the unstable-and-fall-in zones. This relies on the stability 342 properties changing with wetness, thus this strategy will be 343 most successful at an intermediate tilt. 344

To quantify the benefit of a given orientation, we define the following metrics:

$$\mathcal{F}_{\text{unstable}} = 1 - \frac{\mathcal{A}_{\text{stable}}}{\mathcal{A}},$$
 [4]

$$\mathcal{F}_{\text{in-out}} = \frac{\mathcal{A}_{\text{in}} - \mathcal{A}_{\text{out}}}{\mathcal{A}},$$
[5]

where  $\mathcal{F}_{unstable}$  is the fraction of the surface that is unstable, 345 while  $\mathcal{F}_{in-out}$  is the difference between the fraction of the 346 surface that is unstable and for which dynamic motion leads 347 to falling in and the unstable fraction for which dynamics leads 348 to falling out. These are computed for the Flared peristome in 349 Fig. 4(b), with  $\mathcal{F}_{unstable}$  and  $\mathcal{F}_{in-out}$  plotted as green and blues 350 lines respectively, each for 3 different values of  $\mu$ . The unstable 351 fraction increases monotonically, such that almost the entire 352 surface is unstable at the vertical orientation  $\phi = 90^{\circ}$ , while 353  $\mathcal{F}_{in-out}$  shows a non-monotonic relation with tilt. 354

From these metrics, we then compute an efficiency  $\mathcal{E} :=$ 355  $\mathcal{F}_{\mathrm{unstable}} \times \mathcal{F}_{\mathrm{in-out}},$  defined as the product of unstable fraction 356 and 'in minus out' fraction. A surface with perfect efficiency 357  $\mathcal{E} = 1$  is such that every point falls in. Note that with this 358 definition, negative efficiency is possible when more points fall 359 out than in. The efficiency metric is plotted in Fig. 4(c), and, 360 interestingly, we see that  $\mathcal{E}$  has a maximum value near  $\phi = 45^{\circ}$ 361 , for all values of the friction coefficient, the same range as the 362 tilt we have extracted from N. veitchii. 363

Nevertheless, as noted above, not all species exhibit an approximate  $45^{\circ}$  tilt. For instance, the peristome of *N. jacque*lineae is oriented much closer to the horizontal ( $\phi = 0$  in 366 our description). The peristome of *N. jacquelineae* is also 367

distinctly different from that of N. veitchii, with a flatter and 368 more uniform shape, and only a slight gradient towards the 369 center. In Fig. 4(d), we plot the efficiency metric against 370 371  $\phi$  for our model of *N. jacquelineae*. Since the peristome is 372 flat, the surface must become very slippery for any points to 373 become unstable; for this calculation, then, we have set the friction coefficient to zero, so that all points on the surface are 374 unstable. For reference, we also include the same calculation 375 for our model of the Flared peristome. Plotted on this scale, 376 and for a completely slipper surface, the efficiency is nearly 377 constant for N. veitchii, showing only a noticeable decrease 378 at the highest tilt. The efficiency of N. jacquelineae, on the 379 other hand, decreases significantly and monotonically with 380 increasing tilt, reaching negative values before  $\phi = 45^{\circ}$  and 381 with nearly 60% more points falling out than in at vertical. 382 Because the peristome shape is flat, it requires significant 383 wetting to capture any prey. However, the slight gradient in 384 the geometry is best suited for capture with zero tilt; as the 385 peristome tilt increases, a greater number of points slide off 386 the bottom, rather than being guided inward for capture. 387

Our model thus predicts a strong link between tilt and prey capture, but in a non-trivial way, with the optimal tilt itself being a function of the peristome shape. Taken together, these results indicates that tilting may be an adaptation to optimize prey capture efficiency.

# 393 4. On ribs and teeth

All peristome surfaces possess ribs of varying height and wave-394 length. In a handful of species, these ribs are highly con-395 spicuous and tooth-like, e.g. in N. macrophylla, N. diabolica 396 [Fig. 2(d)], N. villosa and N. hamata (not shown). Phyloge-397 nomic data indicate this phenomenon has evolved indepen-398 dently in the genus Nepenthes (15). In this section, we examine 399 the prev-capture benefit that may be obtained from such fea-400 tures, in the context of a cost-benefit analysis. Typically, ribs 401 have sharp peaks and wider smooth valleys. Intuitively, the 402 presence of ribs is beneficial as prey that may have slid off the 403 external pitcher are instead guided into the trap. However, 404 such features increase the area at a potentially substantial 405 energetic cost. Following Section 2, we quantify the energetic 406 cost and benefit trade-off using Eqs. (1) and (2) to define the 407 energetic gain  $E_{\text{gain}}$  in terms of capture area, and energetic 408 cost  $E_{\rm cost}$  in terms of total surface area. As before, these are 409 functions of the total surface area (cost) and surface area for 410 411 which prey slide into the pitcher (gain); for the former, as 412 ribbing features are incorporated into the surface parameterization, we can easily compute the additional area (see also 413 SM Sections 2A and 2C). The metric of relevance is the net 414 energy  $\Delta E = E_{\text{gain}} - E_{\text{cost}}$  [Eq. (3)]. Here, we examine  $\Delta E$ 415 as a function of a single parameter characterizing the size of 416 the ribs/teeth (the wavelength is consistent with observations 417 of living material – see SM Section 1). We first consider the 418 419 presence of ribs within a Flared peristome. In Fig. 5(a), we vary the relative rib height,  $\epsilon := H/W_2$ , (using the measures 420 defined in Fig 2) from  $\epsilon = 0$  (perfectly smooth) to  $\epsilon = 0.033$  -421 the measured value for N. veitchii is  $\epsilon \approx 0.015$ , as indicated on 422 the graph. We have used the same form of energy functions 423 f and g as in Fig. 3(b), and have varied  $c_g$  from 1 to 5. For 424 large values of  $\epsilon$ , the net energy begins to decrease, showing 425 that there is a limit that is reached when the construction cost 426 of increased rib height outweighs the benefit of prev capture. 427



**Fig. 4.** The impact of peristome orientation on prey-capture. (a) A phase diagram showing stability and capture properties for varying friction coefficient  $\mu$  and peristome tilt with respect to the vertical,  $\phi$ , for a model of a flared peristome. Green points are stable, red points slide into the pitcher, and black points slide out. (b) Plots of  $\mathcal{F}_{unstable}$  (green) and  $\mathcal{F}_{in-out}$  (blue) as a function of tilt  $\phi$  for the flared peristome, each for varying values of  $\mu$ , as indicated. (c) Capture efficiency measure as a function of  $\phi$  and varying values of  $\mu$ . Measured orientation for *N. veitchii* is indicated. (d) Efficiency measure as a function of tilt for a fully wetted peristome ( $\mu = 0$ ) for the flared peristome model (bright red) curve and a model of *N. jacquelineae* (dark red) displaying a less flared and more uniform peristome geometry. Red points slide into the pitcher and black points slide out. Measured orientation for *N. jacquelineae* is indicated.

Comparing Fig. 3(b) and Fig. 5(a), we note that for similar 428 values of  $c_a$ , the optimal degree of flaring and ribbing are 429 in rough correspondence with the extracted values from N. 430 veitchii, i.e. our model predicts optimal levels of flaring and 431 ribbing that are consistent with those observed in nature, 432 adding weight to the hypothesis that these features confer a 433 selective advantage in the capture-versus-construction trade-434 off. 435

In Fig. 5(b), we perform the same analysis for a model of 436 a thin peristome with varying teeth heights (still defined as 437  $\epsilon = H/W_2$ ; in the case of large teeth, these correspond to 438 our model of N. diabolica [Fig. 2(d)]. The net energy  $\Delta E$  is 439 plotted against  $\epsilon$  for the same parameter values as in (a). For 440 these values,  $\Delta E$  decreases monotonically with  $\epsilon$  and there is 441 no net energetic benefit associated with producing teeth. The 442 middle plot shows both the fraction of seeded points captured 443 (black) and the total surface area divided by the smooth area 444 with  $\epsilon = 0$  (blue). While teeth do increase the capture fraction, 445 it is only by a small margin, while the area increases by a 446



**Fig. 5.** Impact of ribbing and teeth features on prey capture. (a) Net energy  $\Delta E$  plotted against relative rib height for a model of a flared peristome. Energy parameters are  $\beta_g = \beta_c = c_c = 1$ , with  $c_g$  varying from 1 to 5. Optimal  $\Delta E$  is indicated with a star. Measured ribbing height range for *N. veitchii* indicated. Below: capture properties for a perfectly wetted surface ( $\mu = 0$ ); red points slide into the pitcher, and black points slide out. Zoom in of surface ribbing shown for each height. (b) Net energy  $\Delta E$  plotted against rib/teeth height for a model of *N. diabolica*. Energy parameters are the same as in (a) for the top graph. Middle graph plots both the fraction of the surface on which prey are captured, and the surface area relative to a smooth surface. The bottom graph has the energetic gain coefficient  $c_g$  increased to 50, with other parameters the same. Measured ribbing height range for *N. diabolica* indicated. Right: capture properties for perfectly wetted surfaces ( $\mu = 0$ ); and zoom in to show teeth features at the indicated heights.

factor of 6 over the range considered. In other words, the cost 447 significantly outweighs the benefit. Since the construction cost 448 is considerable, it is possible that teeth serve a function that 449 falls outside the scope of our model, for instance, retention of 450 prey. The ends of the teeth project markedly into the interior 451 pitcher and could form a barricade that could prevent large 452 prey from escaping. We should note that the presence of such 453 a prominent feature can be predicted in our framework, but 454 only if the energetic gain of any increased capture is weighted 455 highly. The bottom graph in Fig. 5(b) plots  $\Delta E$  with  $c_a$ 456 increased from 1 to 50. . Here an interior maximum occurs at 457  $\epsilon = 0.44$ , a teeth height similar to the extracted value for N. 458 diabolica, indicated, though we stress a 50-fold increase was 459 460 required in the energetic gain parameter  $c_g$ .

# 461 5. On peristome size

<sup>462</sup> Finally, we explore the effect of peristome size on the efficiency
<sup>463</sup> of prey capture. Peristome dimensions vary across the genus,
<sup>464</sup> which could be a consequence of divergent selective pressures
<sup>465</sup> from differences in prey size and availability.

The point-mass model is scale-free. Thus, in order to investigate the specific effect of prey size, we consider a minimal representation of a prey with finite size, sitting on a crosssection of a peristome. The peristome is modeled as a circle in a vertical plane, with radius  $R \equiv 1$ , taken to be a reference length. The prey is modeled as a rigid body in contact with the 471 peristome at two points located at the same distance  $\rho$  from 472 the rigid body's center of mass G, and with angle  $2\alpha$  between 473 G and the two contact points [Fig. 6(a)]. The scaled length  $\rho$ 474 defines the length scale of the prey, while  $\alpha$  characterizes its 475 shape (flatter insects have larger  $\alpha$ ). The position of the prey 476 on the peristome is given by  $\theta \in [0, 22.5^{\circ}]$ , the angle between 477 the vertical axis and the prey axis. We assume that the prey 478 is only subject to its own weight, applied at G. As before, we 479 consider dry friction between the prey and the peristome, with 480 coefficient  $\mu$  at both contact points, and we derive the critical 481 angle for stability (see SM Section 3, and Refs. 18, 19). . For 482 each value of  $\rho$  and  $\alpha$ , we compute exactly the maximum angle 483  $\theta_c \leq \alpha$  beyond which equilibrium is lost, and the prey falls. 484 More precisely, for  $\theta_c < \alpha$ , the prey will slip when  $\theta = \theta_c$ , 485 whereas if  $\theta_c = \alpha$  the prey will lose contact and tumble into 486 the trap. The result is plotted in Fig. 6(c), where  $\theta_c$  appears 487 as a color map in the  $\alpha$ - $\rho$  plane . A region in which tumbling 488 occurs is indicated on the left side of the plot, for small  $\alpha$ . 489 The uncolored white region corresponds to disregarded points 490 in which the leg axis would have to penetrate the surface. 491

From the perspective of a prey, Fig. 6(c) shows that it is advantageous to be as flat as possible, in the sense that for any  $\rho$ , the largest stability angle is achieved when  $\alpha$  is maximal. It is also generally the case that very small or



**Fig. 6.** Finite-size prey. (a) Schematic of the two-leg prey model geometry. (b) The two modes of capture: slipping and tumbling. The friction cone with angle  $\theta_c$  characterizes the zone where frictional stability can be maintained for a given prey and friction coefficient  $\mu$ . (c) Density plot showing the size of the stability zone ( $\theta_c$ ) vs prey angle ( $\alpha$ ) and prey size ( $\rho$ ), with  $\mu = 0.5$ . Inset: plot of  $\theta_c$  vs  $\rho$ . for  $\alpha = 45^{\circ}$ . Note that  $\theta_c$  ( $\rho$ ) has a minimum  $\theta_c^*$ , reached at a finite value  $\rho^*$ .

very large prey have an advantage. Indeed, for any  $\alpha$ , the 496 49 stability zone  $\theta_c$  is maximal at the bottom and right edge of the domain (red solid line). This also shows that the point-498 mass model, which corresponds to  $\rho \to 0$ , provides a lower 499 bound for the trapping efficiency. The function  $\theta_c(\rho)$  is 500 non-monotonic, achieving a minimum value at an intermediate 501 size  $\rho$ , denoted  $\rho^*$  (an exact expression is provided in SM 502 Section 3). This is evident from the valley indicated by the 503 black solid line in Fig. 6(c) and from the inset which plots  $\theta_c$ 504 505 against  $\rho$  for  $\alpha = 45^{\circ}$ . Since we have scaled the insect length by the peristome size, the prey size is  $r = \rho R$ . Therefore, 506 there is an optimal peristome size  $R^*(\alpha) = r/\rho^*(\alpha)$  that will 507 be most effective at capturing the prev. Note that, in the 508 slipping regime, the optimum size  $\rho^*$  is independent of  $\mu$  and 509 is, therefore, a universal geometric property of the model. For 510 instance, considering an environment where typical prey have 511 angle  $\alpha = 45^{\circ}$  and size r, and small (but arbitrary) friction 512 coefficient  $\mu \ll 1$ , we have  $\rho^* \approx 0.5$ , and the highest trapping 513

efficiency will be achieved by peristomes with  $R \approx 2r$ , which generates a 17% efficiency gain with respect to the most stable case  $\rho \rightarrow 0$ , all other things being equal. From an evolutionary viewpoint, this observation suggests the existence of a linear scaling law between the peristome size and the typical size of the prey that will be most easily caught in a particular ecological niche.

A few studies (20, 21) have classified prev contents for a 521 range of *Nepenthes* species in a given habitat, and these seem to 522 be consistent with a correlation between larger peristomes and 523 larger prey, e.g. pitchers with small peristomes, on the order 524 of  $R \approx 1$  mm in (N. albomarginata and N. gracilis) almost 525 exclusively captured termites and ants, while pitchers with 526 larger peristomes, on the order of  $R \approx 5$ -10 mm or more (e.g. 527 N. rafflesiana) also captured ants, but also captured a wider 528 variety of other prey, including Gasteropoda, Coleoptera, and 529 Arachnida. However, these data do not include measurement 530 of the actual size of the prey trapped and the trend is therefore 531 only qualitative. Moreover, we note that the scaling law we 532 have derived only considers peristomes with constant curvature 533 in which the prey only slips in the plane of the curve. This 534 approximation should be valid in the case of Flat geometries, 535 or **Base** geometries if the tilting is low enough and/or the ribs 536 are high enough so that slippage occurs in the cross-sectional 537 plane, but is not sufficient to address peristome geometries with 538 significant tilting or flaring. In particular, the larger species 539 in the studies above (N. rafflesiana and N. hemsleyana) tend 540 to have more curvature variation, and thus slipping can occur 541 in different directions at different points on the peristome. 542

## 6. Discussion

The remarkable diversity of trap forms in the genus Nepenthes 544 is emerging as an adaptive radiation analogous to better-545 known examples from the animal kingdom, such as the beaks 546 of Darwin's finches (3). However, the drivers of the adaptive 547 radiation in Nepenthes remain poorly known or unexamined 548 in most species. Indeed, little or nothing is known of the prey 549 captured by most of the ca. 200 known Nepenthes species. 550 The 30-40 species from Borneo are among the best-studied 551 and reveal a diversity of pitcher and peristome morphologies, 552 and prey (22). However the relationships between these di-553 vergent structures, and the prev they trap, remain unclear. 554 By using mathematical modeling and the laws of Newtonian 555 mechanics, our study has provided a theoretical basis for how 556 prey capture may be influenced both by peristome shape and 557 relative size. The diversity of peristomes in *Nepenthes* appears 558 to have evolved in response to dietary needs, adding weight 559 to the hypothesis that a divergence in trap form represents an 560 adaptive radiation. 561

Carnivory evolved independently in five orders of flowering 562 plants in response to nutrient stress. Advances in genome and 563 transcriptome sequencing have revealed the repurposing of 564 defense-related genes is an important trend in the evolution of 565 plant carnivory (23). Nepenthes evolved within a clade that in-566 cludes snap trap leaves in the genera Dionaea and Aldrovanda, 567 in which a touch-sensing mechanism allows rapid closure; and 568 flypaper trap leaves which move more slowly, e.g. Drosera. 569 Active mechanisms represent geometric and mechanical solu-570 tions adapted for specific prev situations; accordingly, a high 571 diversity of trap configurations has evolved across the various 572 niches occupied by carnivorous plants (24). In Nepenthes, 573

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prev capture relies on insects being attracted to, and sliding 574 off, the wet peristome. Attraction is achieved by nectar and 575 coloration, while sliding is achieved both by the surface prop-576 577 erties of the peristome and the peristome geometry. While the 578 surface properties have been well-documented, here we provide 579 the first study linking geometry and mechanics—in this case rigid body Newtonian mechanics-to prey capture. Just as in 580 active traps, efficacy is underpinned by both geometry and 581 mechanics. 582

An optimal geometry might be expected to exist to enable 583 passive capture irrespective of insect type or size. However, 584 we find no such evidence of this; on the contrary, our analysis 585 provides a clear context in which we may understand why peri-586 stome geometry in *Nepenthes* is divergent. We consider the 587 value of a given peristome feature in terms of cost-benefit: the 588 energetic cost of peristome construction against the energetic 589 gains of prev capture. While cost-benefit depends on biotic 590 variables, we provide a hypothetical framework for investigat-591 ing this balance. In the case of peristome flaring, our analysis 592 points to a consistent means by which an evolutionary path 593 from narrow to a flared peristome might exist. Moreover, our 594 595 analysis may also provide an explanation for an evolutionary divergence in peristome geometry. Indeed, a small change in 596 the parameter  $c_q$ , which characterizes the relative energetic 597 gain of increased prey capture, has a strong impact on the 598 optimal flaring, and for some values, the unflared geometry 599 is energetically optimal. As the energy pathways are likely 600 to vary among species, so will the optimal degree of flaring, 601 602 and in this context, it is not surprising that not all species possess widely flared peristomes. A similar situation exists 603 in the case of ribbing or teeth features which may generally 604 serve to increase the prev capture functionality, albeit at high 605 production costs. Considering peristome orientation with re-606 spect to gravity, our analysis also provides a plausible physical 607 608 explanation for the correlation between geometry and orientation, demonstrating that a wider and more uniform peristome 609 has better capture efficiency when oriented horizontally. 610

In these examples, capture success was linked to geometric 611 complexities, and a detailed geometric description was needed 612 for which we sacrificed prey complexity in the description. 613 Conversely, we analyzed finite-sized prey with multiple contact 614 points on a simplified, constant curvature surface restricted to 615 two dimensions. Here again, the connection between geometry 616 and prey specifics was evident and we identified a nonlinear 617 relationship between prey geometry and capture efficiency. 618 Taken together, these results suggest a fine-tuning of peristome 619 size to optimize prey capture likelihood for a given shape and 620 size. 621

The two distinct forms of analysis we have presented each 622 incorporate simplifications in different ways. Amalgamating 623 the approaches, i.e. combining three-dimensional geometries 624 with a detailed description of finite prey possessing multiple 625 surface contact points, would be more powerful; though it poses 626 a significant challenge to do so in a tractable manner. While 627 our analysis focused on the functional benefits of peristome size 628 and geometry, another problem concerns the developmental 629 process underlying a particular functional geometry. Therefore, 630 a complementary direction of future research would be the 631 morphogenesis of the peristome. 632

The striking divergence of pitcher forms in Nepenthes sug-633 gests that they should attract different prey across their various 634

habitats. Prev capture is also known to shift with altitude. 635 Many lowland species are attractive to ants, and possess waxy 636 interior pitcher surfaces effective for capturing these insects 637 (9, 25). By contrast, montane species, which tend to have 638 viscoelastic pitcher fluids, are more effective at trapping flying 639 prey (10, 26). Beetles appear to be the most abundant prey 640 for N. villosa, a montane species with conspicuous teeth (20). 641 Peristome teeth may play a role in the retention of bulky prey; 642 however, data from other species with prominent teeth are 643 lacking. Different combinations of pitcher surface and fluid 644 properties probably correlate with peristome size and geometry. 645 For example, pitchers without waxy surfaces often produce 646 larger and more inward-sloping peristomes (25). Importantly, 647 diversity in pitcher form is also probably linked to a vicariance 648 driven by the complex geology and geography of Southeast 649 Asia. Clarke and Moran (27) show that patchy distributions 650 with distinct climates may have contributed significantly to 651 a variation in pitcher form. Soil type too, is likely to have 652 influenced local plant community structures, generating spe-653 cific environmental niches to which the various Nepenthes 654 species may be locally adapted. These factors are likely to 655 have played an important part in the evolution of peristome 656 size and geometry. Despite its central role in capture, we 657 know virtually nothing about how prey shifts with changes 658 in peristome morphology. Further work would benefit from 659 empirical and observation data on prey capture from across a 660 range of pitcher and peristome forms in different habitats. 661

Our study provides a mathematical construct for quan-662 titatively linking geometry to prey capture. There are two 663 distinct steps underlying this link: first is the translation 664 of a given peristome surface to a mathematical object (a 665 surface), and second is the analysis of prey capture on that 666 idealized object. With regards to the former, the surface 667 measures we have defined in Fig. 2(e) provide a direct 668 means of quantifying peristome properties that can then 669 be mapped to prey capture success via the second step, a 670 general mechanism through which inter- and intra-specific 671 variation in geometry and prey capture can naturally be 672 studied. Though this map may be improved in future work 673 by directly incorporating peristome curvature measures, 674 which we have shown to have significant importance in prey 675 capture success. Investigating this link empirically is a 676 crucial next step. Of course, prey capture will also depend 677 on variables beyond geometry, such as coloration and nectar 678 production. Furthermore, pitcher morphology usually varies 679 with plant age (traps produced by young rosettes are distinct 680 from those on mature vines). In principle, our conceptual 681 approach can accommodate the inclusion of such features. 682 This highlights the value of mathematical modeling as an 683 iterative process that can both motivate and adapt to new 684 empirical studies. In conclusion, this approach provides a 685 platform for testing hypotheses on the evolution of nature's 686 green predators: some of the plant kingdom's greatest enigmas. 687

Data availability. *Mathematica* notebooks reproducing model 689 output are available in the public depository: https://ora.ox.ac. 690 uk/objects/uuid:a7bf597d-07ac-49b0-a444-5b3343618c22.

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