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Low floristic richness of afro-alpine vegetation of Mount Kenya is related to its small area

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Abstract

Diversity patterns of tropical alpine vegetation is poorly studied. We estimated vascular plant floristic richness for two typical afro-alpine communities in Mount Kenya using a series of nested plots sized from 25 to 100 m². The α -diversity was low for all plot sizes (4.8–7.8 and 12.8 species per one and 100 m², respectively). Comparative analysis of α -, β - and γ -diversity across 22 plant communities from five Mountain regions (Mount Kenya, European Alps, Caucasus, Tibet, New Zealand Alps) revealed that area of mountain system was the only significant variable shaping the local richness; this effect became stronger with increasing spatial scale. Beta-diversity, by contrast, showed neither latitudinal trends nor significant correlation with other geographical or climatic variables. We conclude that the total area of mountain system is one of the main factors determining the regional species pool and, ultimately, the local diversity of alpine plant communities (the "echo-effect"). Small area and isolation of Mt. Kenya are considered as the main reasons for low local richness of its afro-alpine vegetation.

Keywords Species–area relationship \cdot Floristic richness \cdot Alpha-diversity \cdot Beta-diversity \cdot Mt. Kenya \cdot Afro-alpine \cdot Tropical alpine \cdot Plant communities

Introduction

Understanding spatial variation in biodiversity along environmental gradients is one of the central themes in ecology (Rosenzweig 1995). The mechanisms underlying these gradients are, however, often difficult to distinguish because multiple processes operating at multiple scales may influence different diversity components (i.e., α -, β - and γ -diversity) and thus shape the species–area relationships (SAR). The form of the SAR is known to be influenced also by the scale and sampling design (Azovsky 2011; Scheiner et al. 2011; Storch 2016).

In particular, floristic richness (α -diversity, number of species per unit area or plot) depends on three main groups of factors, namely total area, age of landscape and recent ecological regime (Zobel et al. 2011; Wilson et al. 2012;

Chytrý et al. 2012, etc.). These factors, on the one hand, determine regional species pool as a source of species for a local community, and, on the other hand, constitute the biotic and abiotic filters screening species from this pool on community level (Belyea and Lancaster 1999; Zobel et al. 2000; Triantis et al. 2008). Floristic richness of a plot increases with local and regional species pools (Partel et al. 1996) and with the total area occupied by the community in a landscape (Onipchenko and Pavlov 2009; Zobel et al. 2011). Age of a community generally increased the plant species richness, since more species have time to arrive into older community (Grubb 1986; Bengtsson et al. 1994; Zobel et al. 2011; Cowling et al. 2015). Communities which are small in area or occupy more extreme ecological conditions (for example, water-saturated peatlands) are poor in vascular plants (Onipchenko and Semenova 1995; Onipchenko et al. 2005).

Due to its isolated position and a relatively young alpine flora, the East African alpine vegetation is not very rich and includes a total of about 500 alpine species from 190 genus, or about 174 species per mountain (Sklenar et al. 2014; Gehrke and Linder 2014). Vegetation of Mt. Kenya is well studied (Rehder et al. 1988; Young and Peacock 1992),

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and gives a good example of afro-alpine vegetation in east Africa, with a total alpine flora of 269 species (Gehrke and Linder 2014). Alpine tops of East-African Mountains are "islands" of cold climate vegetation surrounded by mountain forests and savannas (Gehrke and Linder 2014). We may thus expect low floristic richness in small plots of afro-alpine vegetation according to "island effect" (MacArthur and Wilson 1967). On the other hand, volcanos in East Africa are relatively young, for example, the eruption of Mt. Kenya happened 2.6-3.1 million years ago in late Pliocene (Gehrke and Linder 2014; Mizuno and Fujita 2014). In contrast to temperate areas, the rate of speciation in tropics is less intensive in low productive areas (Zobel et al. 2011) such as alpine zones where plant growth is limited by low temperatures (Körner 2003). Alpine flora of Mt. Kenya is more clustered phylogenetically than the Kenyan flora of other altitudinal belts because "the environmental stress acted as a filter on lineages due to lower temperatures and unstable climate "(Zhou et al. 2018: 8936). At the same time, there are some indications that mountain communities show an increase in species turnover along altitudinal and latitudinal gradients due to the greater intra-annual temperature stability of tropical mountains, increased endemism and smaller range sizes of tropical species (Ghalambor et al. 2006; Qian and Ricklefs 2007; McFadden et al. 2019). This trend in β -diversity across biogeographic gradients could also be caused by corresponding variations in regional species pool (γ -diversity) by purely statistical reasons (Kraft et al. 2011; Myers et al. 2013). Thus, Mt. Kenyan communities could be expected to show lower α -diversity but higher β -diversity, in comparison with subtropical or temperate alpine regions. However, neither comparable estimations of plant diversity components nor parameters of species-area relationships for this region have been investigated so far.

In this study, we aimed (1) to evaluate floristic richness of vascular plants in two afro-alpine communities (*Carex*-Fen-Community and *Lobelia telekii-Dendrosenecio keniodendron*-Community) situated along an altitudinal gradient in the western area of Mt. Kenya, (2) to compare it with richness of temperate alpine communities, and 3) to analyze the possible factors shaping the local diversity of alpine communities across the tropics-to-temperate gradient.

Materials and methods

Site description

the alpine belt consists of alpine meadows and shrublands (Coe 1967).

Climate of this area is of a tropical diurnal type, which Hedberg (1964) described as "winter every night and summer every day". The annual mean temperature at 4191 m is $1.7 \,^{\circ}$ C with a mean daily range of $9 \,^{\circ}$ C for January and July. Mount Kenya has two wet seasons and two dry seasons as a result of the monsoon. From mid-March to June and From October to December the mountain receives approximately a 5/6th of the annual precipitation (900–2500 mm per year) (Coe 1967). Soils are structureless, with inclusions of stones, carbon content of 7–10% and a pH of 4.9–5.1.

We studied two adjacent plant communities in the upper alpine belt. The first community was *Carex*-Fen-Community (CF) corresponding to *Carex*-Bog-Community according to Rehder et al. (1988) or community of "valley floors" described by Coe (1967). The community occupies valley bottom with highly moistened soils, almost flat ground adjacent to streams (4162–4172 m). The most frequent species are *Carex monostachya*, *Festuca pilgeri*, *F. abyssinica*, *Ranunculus oreophytus*, *Haplocarpha rueppellii*, *Haplosciadium abyssinicum*.

The second community was *Lobelia telekii-Dendrosenecio keniodendron*-Community (LD) (Rehder et al. 1988). Coe (1967) called this as a "valley walls" community. It occupies slopes of the valley with damp, well-drained ground (4234–4252 m). The most abundant herbaceous species are *Dendrosenecio keniodendron, Lobelia telekii, Festuca pilgeri* and *Alchemilla argyrophylla*. For this community, some of the soil properties include the following: total N 0.77–0.93%, C 14%, Mehlich III extraction P 25–55 mg/kg, K 568–584 mg/kg, Ca 2400–3400 mg/kg, Mg 357–360 mg/kg (M. Zobel, personal communication).

Field methods

For each of the two communities, a series of sample plots, based on the design of Onipchenko and Semenova (1995; Fig. 1), were selected at sites considered representative of the particular vegetation belt. Each series consisted of nested plots with sides of 5, 10, 25, 50, 100 cm (four replicates each), 200, 500 and 1000 cm (one replicates each). Five series were examined in each community type, thus providing five replicates for larger (4, 25 and 100 m²) plots and 20 for each of the smaller ones (total studied area 500 m² for each community). Only the number of vascular plant species was recorded.

Data analysis

Floristic richness (mean number of vascular species per plot and standard errors as variation parameters) was calculated for all eight plot sizes in each of the two communities. Five



Fig. 1 Sampling scheme with plots from 0.0025 to 100 m^2 (after Onipchenko and Semenova 1995, 299–304)

hierarchically organized diversity measures were estimated: two levels of α -diversity (mean species number per 1 m² (S_1) and 100 m² (S_{100})); two levels of β -diversity ($\beta_{100} = S_{100}/S_1$ and $\beta_{500} = S_{500}/S_{100}$); and total species number in 500 m² (S_{500} as γ -diversity estimator).

To evaluate the representativeness of the data obtained from each community, we constructed the combined species accumulation curves basing on average number of species for each number of 1, 25 and 100-m^2 replicates. We also applied Chao-2 correction for rare species (Chao 1987) to predict the in a community.

To construct the SAR curves, two different approaches were used. First, the curves were built separately for each set of nested plots (spatially explicit SAR, in terms proposed by Scheiner (2003) and Scheiner et al. (2011)), and then the values of SAR parameters were averaged. Alternatively, the curves were built using number of species averaged overall plots of each particular size, ignoring their spatial arrangement (noncontiguous, not spatially explicit SAR).

To fit the curves, two models, Arrenhius's (1921) power function (1) and Gleason's (1922) logarithmic function (2) were used:

$$S = c \times A^{z}, \tag{1}$$

$$S = a + b \times \ln(S),\tag{2}$$

where S = number of species in area A; a, b, c, z are regression parameters; coefficients "c" and "a" of Eqs. (1) and (2) show the number of species per unit area (1 m²); exponent "z" and coefficient "b" show the rates at which species richness increases with area.

Non-parametric two-tailed Mann–Whitney U test was applied for comparing diversity values between communities, Fisher z test—for checking the equality of correlation coefficients, and Student *t* test—for comparing the parameters of SAR curves.

To analyze dependence of species richness parameters on geographical position and climate features, we combine our data with the values from four other mountain regions (European Alps, Caucasus, Tibet, New Zealand Alps) where we used exactly the same method as in the present study (Onipchenko and Semenova 1995; Onipchenko et al. 2005, 2014).

As predictor variable, we use the total mountain area (data obtained from the electronic "The Mountain Biodiversity Portal" (Körner et al. 2017); in Tibet mountain region within the meaning of Gurung (1999) we included Tibetan Plateau and others adjacent ranges with near-continuous alpine zone). Also we applied altitude and latitude of localities studied, mean annual temperature and precipitation (based on WorldClim v.2 1-km spatial resolution climate surfaces, Fick and Hijmans 2017). As another proxy of alpine area for different mountain systems we used mountain range (received from the mountain polygons available at the same source) and ran ordinary least squares linear regression between this parameter and mean number of species per 100 m^2 for all studied communities within mountain region.

Non-parametric distance-based regression analysis (DistLM) was used to explore the relationships between variations in α -, β - and γ -diversity among these mountain systems and six predictor variables: total area of a mountain region (km², logarithmically transformed), altitude and latitude of studied localities, square of latitude (to account possible non-linearity of the relationship), mean annual temperature and precipitation. The values of α - and γ -diversity were also logarithmically transformed prior to analysis, and Euclidean distance was used as dissimilarity measure. Step-wise selection procedure based on Akaike Information Criterion was applied to choose the best set of predictors.

The DistLM and the analyses of species accumulation curves have been performed in PRIMER v. 6.1.15 software (PRIMER-E Ltd, Plymouth, United Kingdom).

Results

Diversity of the Mt. Kenya alpine communities

On plots of both communities (total area 1000 m^2) we found totally 28 vascular plant species, which is about 10% of Mt. Kenya alpine flora (269 species according to Gehrke and Linder 2014).

For the CF community, the species accumulation curves increased with obvious deceleration (Fig. 2a). The expected total number of species, estimated by Chao-2 method, became stabilized at the level of 16–17 species, close to the actually observed figure, indicating that the



Fig. 2 Species accumulation curves for CF (**a**) and LD (**b**) communities. Observed number of species (solid line) and Chao-2-corrected values (dotted line) are shown

community was adequately sampled and captured the full plant richness of the target area. For the LD community, however, the accumulation curves were still rising without deceleration, as well as the Chao-corrected estimators (Fig. 2b). This indicates that full plant richness of this community is potentially high, and it is reasonable to expect up to 25–26 species with further sampling in this area. This difference is nevertheless is small enough to consider the data on this community representative, too.

Both spatially explicit and not spatially explicit types of SAR had practically identical parameter values indicating no intraspecific spatial aggregation of individuals (Scheiner et al. 2011), so hereinafter we did not discuss they separately but provided only the results for the latter one.

Both power and logarithmic functions fit the data rather well. According to both models, number of species increased slightly faster in LD than in CF, though the slopes differed significantly only for the power model (Table 1). Two alpine communities differed noticeably in floristic composition and structure, having only 9 species in common. Floristic richness in LD on smaller plots (1-m² and smaller) was significantly lower than in the CF community, possibly due to smaller plant size in the fens with low abundance of mega rosette trees. For 1-m² plots, mean α -diversity values were 7.8 and 4.8 species for CF and LD communities, respectively (Table 1). At the same time, the LD community demonstrated higher β -diversity, both within and between 100-m² plots, indicating higher spatial heterogeneity at a range of scales; though the difference between β_{500} values was insignificant (Table 1). This heterogeneity, also confirmed by steeper SAR slopes for LD community, resulted in equal mean floristic richness on 100 m² plots: 12.8 species for both communities.

 Table 1
 Species diversity of vascular plants in different plots and

 SAR parameters for the two contrasting alpine plant communities on
 Mount Kenya, Kenya

Plot area, m ²	N	Mean floristic richness $(\alpha$ -diversity, species per plot) \pm std. err.		р
		CF	LD	
0.0025	20	1.4 ± 0.15	0.8 ± 0.12	0.0046
0.01	20	2.65 ± 0.26	1.2 ± 0.16	0.0001
0.0625	20	4.7 ± 0.25	2.35 ± 0.24	0.0001
0.25	20	6.5 ± 0.32	3.45 ± 0.29	0.0001
1	20	7.75 ± 0.35	4.80 ± 0.30	0.0001
4	5	10.6 ± 0.93	9.0 ± 0.45	0.111
25	5	12.0 ± 1.34	11.4 ± 0.6	0.384
100	5	12.8 ± 0.86	12.8 ± 1.16	0.916
Total number of s on 500 m ²	species	16	20	n/a
β -Diversity \pm std.	err.			
β_{100}		1.665 ± 0.200	2.711 ± 0.621	0.012
β_{500}		1.275 ± 0.207	1.614 ± 0.318	0.063
$S = c \times A^z$				
с		6.760 ± 1.093	4.668 ± 1.064	0.214
z		0.202 ± 0.025	0.275 ± 0.017	0.033
r^2		0.914	0.976	0.297
$S = a + b \times \ln(A)$				
а		8.092 ± 0.176	6.576 ± 0.466	0.010
b		1.143 ± 0.050	1.227 ± 0.132	0.563
r^2		0.989	0.935	0.161

N, number of samples; CF, *Carex*-Fen-community; LD, *Lobelia tel-ekii-Dendrosenecio keniodendron*-community; *p*, significance of differences between CF and LD; n/a, test not available

Cross-region analysis of diversity patterns

We analyzed the variation in α -, β - and γ -diversity from 22 alpine communities in five mountain regions (European Alps, Caucasus, Tibet, New Zealand Alps and Mt. Kenya) where exactly the same sampling methods were applied. The characteristics of the regions are presented in Table 2.

All three measures of local diversity (α_1 , α_{100} and γ_{500}) showed weak but significant positive latitudinal trend, i.e., increased from equator to temperate areas, while the measures of species turnover (β_{100} and β_{500}) were not correlated with latitude (Table 3). Neither β_{100} nor β_{500} were correlated with γ -diversity (r=0.104 (p=0.646) and r=0.349(p=0.111), respectively).

Non-parametric regression analysis (DistLM) revealed the strong positive effect of mountain system size on species richness (Table 4). Percentage of richness variability, explained by mountain system size, increased with spatial scale from 47% for 1-m² plots up to 69% for 500-m² area. This relationship was very close to power law (linear in

Mountain system	State	Altitude, m	Latitude	Longitude	Total area, 10 ³ km ²	MAT, °C	MAP, mm	Number of stud- ied communities	S_1	S_{100}	S_{500}	2	References
Caucasus	Russia	2750	43° 26.5′ N	41° 41.3' E	93.2	-1.6	1330	7	9.9–25.0	23–57	43–88	0.179-0.298	1
Alps	Switzerland	2200	46° 47° 1' N	9° 53.5′ E	154.0	-1.3	1319	6	11.1-26.8	23-51	46–98	0.180 - 0.249	1
South Alps	New Zealand	1200	45° 42.1' S	167° 24.6' E	44.1	6.0	2533	c.	6-12	21–24	33–35	0.280-0.437	2
Tibet	China	4100	33° 10.1' N	103° 42.5' E	616	3.2	707	4	10.6 - 39.9	27-81	58-152	0.219-0.328	3
Kenya	Kenya	4200	0° 01.0' S	37° 17.1' E	1.3	10.0	1499	2	4.8-7.8	12	17 - 20	0.196-0.272	This paper

 Table 3
 Strength of latitudinal diversity gradient for 22 alpine communities

Diversity measure	r	р
Alpha (1 m ²) (log-transformed)	0.458	0.032
Alpha (100 m ²) (log-transformed)	0.480	0.024
Gamma (500 m ²) (log-transformed)	0.523	0.012
Beta (1/100 m ²)	-0.060	0.790
Beta (100/500 m ²)	0.230	0.303

r Pearson' correlation between diversity values and latitude, p significance level

double-log axes, Fig. 3a). None of the factors examined, neither geographical nor climatic, had a noticeable effect on β -diversity, except for a weak and insignificant positive relationship between β_{500} and mountain area.

Linear regression of mountain range and mean number of species per 100 m² for all studied communities within mountain region showed very close relationship between these parameters ($r^2 = 0.939$, p = 0.006, Fig. 3b).

Discussion

We studied vascular species richness in two high-alpine plant communities in the Teleki valley on Mount Kenya. These communities turned out to be very similar in floristic richness, despite significant differences in their location, relief, water regime and species composition (only 28.6% of species were found in both communities).

Both power and logarithmic SAR models fit the empirical datasets rather well, explaining over 90% of variations (Table 1). The differences in the correlation coefficients, however, are insignificant, both between communities and between the models, disallowing us to give preference to one of models. When we extrapolated Arrenhius's power function for the whole Mt. Kenya National Park (715 km2), we obtained as high species richness as 415 species for CF or 1271 species for LD. Both values are higher than real estimation of 269 species (Gehrke and Linder 2014), but the first value is quite close. Extrapolation by Gleason's logarithmic function predicted only 31 and 32 species for CF and LD parameters, respectively-much lower than the real value. These results are in good agreement with an observation that logarithmic SAR function could better describe empirical data at small scales up to 100 m² but strongly underestimates richness at larger scale, while power function more universal tends to overestimate large-area richness (Rosindell and Cornell 2009). These divergent results of extrapolation the simple models up to larger scales indicate possible nonmonotonic (triphasic) form of the SAR at broad range of scales (Storch 2016).

Table 4Results of step-wiseDistLM regression analysis.Only the predictors selected byAkaike information criterion(AIC) are presented

Variable (diversity measure)	"Best fit" predictor	AIC	Pseudo-F	р	% of variance explained	
Alpha (1 m ²) (log-transformed)	log area	- 76.05	17.396	0.002	46.5	
Alpha (100 m ²) (log-transformed)	log area	-86.08	29.94	0.001	60.0	
Gamma (500 m ²) (log-transformed)	log area	-87.12	43.91	0.001	68.7	
Beta (1–100 m ²)	No significant effects found					
Beta (100–500 m ²)	log area	-46.88	2.67	0.119	11.8	

Pseudo-F Fisher' criterion, p significance level

(a) Number of species per 500 m^2 100 10 1 000 10 000 600 000 100 000 Mountain area, km² (b) 70 Number of species per 100 m^2 60 50 40 30 20 R²=0.939, p=0.006 10 0 0 500 1000 1500 2000

Length of the mountain chain, km

The SAR slopes (z values in Eq. 1) differed between the studied communities (0.202 and 0.275 for CF and LD, correspondingly), but they are within typical values reported for this spatial scale (for example, 0.12–0.31 for different communities in Curonian Spit (Dolnik and Breuer 2008). Our values are a little bit higher than global z for all biomes (0.18—Whittaker and Matthews 2014), but they are close to mean z for "habitat islands" within large land

areas (0.22—Matthews et al. 2016). So, in contrast to low floristic richness of the studied communities, obtained z values are average for terrestrial vascular plant communities. They are also in the range of values obtained by the same method for Alps, Caucasus and Tibet alpine communities (Table 2, Onipchenko et al. 2014), but lower than the values for New Zealand alpine communities (Onipchenko et al. 2005).

Fig. 3 α -Diversity depends on mountain size. a Relationship between mean number of vascular plant species per 500 m² and mountain system area (r^2 =0.668, p < 0.0001), b relationship between mean number of vascular plant species per 100 m² within the region and mountain system length (r^2 =0.939, p=0.006)

Numbers of vascular plant species per 1-m² plot in Mt. Kenva are among lowest values obtained in similar researches in other alpine communities (Table 2). Low values were noted for New Zealand alpine communities as well due to their real island position (Onipchenko et al. 2005). The highest floristic richness for 1 m^2 (89 vascular plant species) was shown once for mountain grassland in Argentina (Cantero et al. 1999; Wilson et al. 2012). This value is more than tenfold higher than our values. On the other hand, low species numbers for such plots were obtained in Tibetian alpine fens (less than 10 species) (Tsuyuzaki et al. 1990), in polar deserts of Canada (Levesque 1996), alpine screes and snowbeds in Alps (Kammer and Mohl 2002; Vonlanthen et al. 2006). One may suggest that low diversity is connected with harsh ecological conditions, but it does not seem the true for afro-alpine communities. In tropical Andes mean floristic richness of alpine communities (about 40 but up to 68 species per 1 m²) is 5–10-fold higher than in Kenya under similar alpine tropical conditions (Cuesta et al. 2017).

Species richness of studied communities for 100 m² plots was low as well (mean 12.8 species). This value is 20-fold lower than absolute maximum observed value for such plot size in tropical rain forest of Costa Rica (233 species, Whitmore et al. 1985). Our values are also lower than 100 m² vascular plant species richness for grasslands in New Zealand (17-19 species) (Wilson and Sykes 1988), mountain grasslands in Australia and Tasmania (28-32 species) (Minchin 1989), alpine meadows in Altai (15–25 species) (Sedel'nikov 1979), lowland grasslands of Bohemia, Czech Republic, (about 40 species) (Moravec 1973) and the Caucasus (24-80 species) (Tanfil'ev et al. 1979). Our values were, however, close to those reported in alpine tundra of Central North Asia in Kuznetskii Alatau, Russia (10–12 species) (Sedel'nikov 1979) and Northeast Asia in Priokhot'e (9-27 species) (Shlothauer 1990). The last values can probably be explained by the low number of high alpine species in the regions and climatic severity (mean annual temperature in Toko weather station, -11.2 °C (Shlothauer 1990). But as we noted before, alpine tropical environment per se cannot be reason for the low floristic richness in the rich alpine flora of tropical Andes (Cuesta et al. 2017).

In general, we have confirmed our hypothesis about low floristic richness of afro-alpine communities at local scale (up to 500 m²). Comparative analysis across five mountain systems, however, reveals that the only significant variable shaping the local richness is not latitude but the area of mountain system; this effect becomes stronger with increasing the spatial scale. The most probable mechanism of this relationship is that larger area (and higher regional-scale environmental heterogeneity) result in larger regional species pool, which, in its turn, leads to higher local richness (so called "Echo effect", Rosenzweig and Ziv 1999). So, we consider the small total area of alpine vegetation on Mt. Kenya to be the main reason of its low floristic richness.

Very close linear relationship between the length of mountain system and mean species richness per 100 m^2 may indicate that due to linear nature of a mountain range the length is better proxy for *alpine* area and total alpine flora of a region. But this remains a challenge for the future.

Counter to our expectations, the values of β -diversity, both estimated at small (1–100 m²) or larger (100–500 m²) scale, showed no significant latitudinal trends and not correlated with other geographical or climatic factors. They also did not correlate with γ -diversity, so the hypothesis that β -diversity across broad biogeographic gradients is driven by γ -diversity (Kraft et al. 2011; Myers et al. 2013) is not supported by our data. Therefore, small-scale spatial heterogeneity of alpine communities is driven by other, most likely, local factors.

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Author contributions VGO, NAK, AMK and JMN designed the research, VGO, AMK and JMN conducted the research and VGO, NAK, AMK, TGE, AA, SVD and JMN analyzed the data and wrote the article.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any data collected from human participants or animals and, therefore, did not require any ethical approval.

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