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Environmental stress increases out-group aggression and intergroup conflict in humans

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Peaceful coexistence and trade among human groups can be fragile and intergroup relations frequently transition to violent exchange and conflict. Here we specify how exogenous changes in groups' environment and ensuing carrying-capacity stress can increase individual participation in intergroup conflict, and out-group aggression in particular. In two intergroup contest experiments, individuals could contribute private resources to out-group aggression (versus in-group defense). Environmental unpredictability, induced by making non-invested resources subject to risk of destruction (versus not), created psychological stress and increased participation in and coordination of out-group attacks. Archival analyses of interstate conflicts showed, likewise, that sovereign states engage in revisionist warfare more when their pre-conflict economic and climatic environment were more volatile and unpredictable. Given that participation in conflict is wasteful, environmental unpredictability not only made groups more often victorious but also less wealthy. Macro-level changes in the natural and economic environment can be a root cause of out-group aggression and turn benign intergroup relations violent.

This article is part of the theme issue 'Intergroup conflict across taxa'.

1. Introduction

Humans operate in groups of familiar others that, in turn, exist next to other groups. Although peaceful coexistence among neighbouring groups is frequently observed [1–3], peaceful intergroup relations are also fragile—it takes only a few individuals in one group to initiate competition with another group and to ignite violent conflict [4–8]. Identifying the reasons for conflict-initiating out-group aggression elucidates the root causes of conflict among human groups and societies and can help to regulate, if not prevent conflict and its waste.

Theory and research on conflict within and between human groups identified a suite of conflict-provoking elements that reside within the intergroup system and are endogenously created and reinforced by past intergroup interactions. There is good evidence, for example, that past conflicts perpetuate in spiteful desire for revenge [6,9], prejudicial misperceptions [10–12] and feelings of in-group superiority and thwarted entitlements [13,14]. Alone and in combination, such psychological states fuel and enable out-group aggression and intergroup conflict [15,16]. As such, past work explains why conflict between human groups easily escalates and why returning to peaceful coexistence can be difficult. What remains poorly understood, however, is why out-group aggression emerges in the first place. Why would groups of people aggress other groups when there is no history of conflict or no disadvantageous inequalities in the distribution of and access to resources?

One possibility, which we examine here, is that out-group aggression can be triggered by factors outside of the intergroup system, like instabilities of the environment and resource availability. If true, changes in environmental predictability and resource availability would explain when and how peaceful coexistence among human groups and societies transitions to violent conflict. Evidence for this possibility would reveal exogenous changes in the environment as a root cause of out-group aggression, and fit observed linkages between macro-level climate change and economic volatilities on the one hand, and the prevalence of political violence, riots and civil wars on the other [17–22]. It would also resonate with work on non-human primate groups engaging in territorial conflicts for food and mating opportunities [23–27].

The starting point in our analysis is that groups operate in a natural, economic and political environment that can be volatile and unpredictable [28,29]. Environmental degradation and resource scarcities alongside erratic and unpredictable fluctuations in living conditions can thus create carrying-capacity stress—situations where the supply of resources is expected to fall short of what groups need or are used to [30–33]. This can have two consequences. First, under environmental threat and unpredictability people form more cohesive groups [34–38] and increase their cooperative contribution to group survival and prosperity [39–41]. Second, and partly because of increased group cohesion and interdependency, group members distance themselves from other groups [36,37,42,43]. Alone and in combination, these processes would lead to in-group bounded, parochial cooperation that serves the in-group and prevents the consumption of resources by members of other groups [9,30,44,45].

Carrying-capacity stress may also motivate parochial competition—tendencies to compete against and harm (members of) out-groups more than (members of) the in-group [9,30,44,46–48]. For example, economic downturn has been associated with increased xenophobic sentiments and inter-ethnic conflict [43,49,50], a rise in nationalistic sentiments [51] and stricter policies for immigration and international trade [49,50,52]. The reason for such increased parochial competition is, first, that environmental threat and unpredictability can make investing in conflict economically more attractive. Resources spent on fighting are typically lost and such ‘investments’ give an uncertain return—even in the case of victory, the spoils of war may only partially off-set the personal contributions made. In unpredictable environments, however, the prospects of appropriating resources from others may compensate for the uncertainty around resource appropriation from the environment. In addition, carrying-capacity stress may lead people to perceive out-groups as comparatively less deserving and entitled [31,53], rendering it justified to contribute to out-group attack and exploitation [54]. Second, carrying-capacity stress may increase vigilance for outside threat, human enemies included [4,42,55,56]. Possibly, carrying-capacity stress leads individuals to contribute to defending the in-group against possible out-group aggression. Accordingly, carrying-capacity stress may lead individuals to contribute private resources to out-group aggression, and perhaps also to in-group defense. It is out-group aggression in particular that ignites and escalates costly intergroup conflict [4,57,58].

We examined whether and how environmental unpredictability and ensuing carrying-capacity stress conditions out-group aggression and in-group defense with experimental contests between attacker and defender groups [4,58,59], and

with archival data on militarized disputes between revisionist states aggressing their non-revisionist neighbouring states [59–61]. Across both levels of analysis we find that environmental unpredictability triggers out-group aggression and does not condition in-group defense.

2. Intergroup contest experiments

Our experiments implemented intergroup attacker–defender contests (IADC) [4,58,59]. Six individuals were randomly divided into a three-person attacker group and a three-person defender group. Within each group, each individual i received 20 Experimental Euros from which they could contribute g ($0 \leq g_i \leq 20$) to their group’s pool C ($0 \leq C \leq 60$). Individual contributions to the pool are always wasted. However, when $C_{\text{attacker}} > C_{\text{defender}}$ the attacker wins the remaining resources of the defender ($60 - C_{\text{defender}}$), which is divided equally among attacker group members and added to their remaining endowments ($20 - g_i$). Defenders thus earn 0 when their attackers win. However, when $C_{\text{attacker}} \leq C_{\text{defender}}$ defenders ‘survive’ and individuals on both sides keep their remaining endowment ($20 - g_i$). Individual contributions in attacker (defender) groups thus reflect out-group attack (in-group defense) [58].

We created (un)predictable environments by exposing individuals in attacker and/or defender groups to a risk of destruction u of their personal endowments (with $0 \leq u \leq 1$), analogous to farmers being uncertain about crop yields, or investors being uncertain about the return on their shares [16,20,28,29,31,32]. If environmental unpredictability increases vigilance, we should see increased conflict expenditures in defender groups when their risk to private property $u > 0$. If environmental unpredictability increases willingness to exploit, we should see increased conflict expenditures in attacker groups when their risk to private property $u > 0$.

The IADC has a unique Nash Equilibrium in mixed strategies [4,58]. Taking the groups as units, with each group being endowed with $20 \times 3 = 60$ resources, and assuming individuals are risk-neutral rational selfish payoff maximizers, the strategies played in equilibrium imply an average investment in out-group attack (in-group defense) of 5.41 (7.25), and attacker victory in 37.5% of the contest rounds [57,58] (also see SI in the electronic supplementary material). Our experimental manipulation of environmental unpredictability shifts the expected value of contributing to attack and defense upward relative to not contributing. Specifically, when $u = 0.40$, the strategies played in equilibrium imply an average investment in out-group attack (in-group defense) of 10.25 (10.19). Because our manipulation of environmental unpredictability ($u = 0$ versus 0.4) decreases the expected value of keeping resources, it follows that environmental unpredictability should increase out-group attacks. The game-theoretic analyses also show that environmental unpredictability disproportionately increases out-group attack relative to in-group defense, and attacker victory increases to 53.15% in equilibrium. These game-theoretic predictions provide a benchmark against which we can compare investment in out-group aggression and in-group defense in (un)predictable environments. Deviations from these benchmark values would point to additional psychological processes induced by environmental unpredictability, including increased

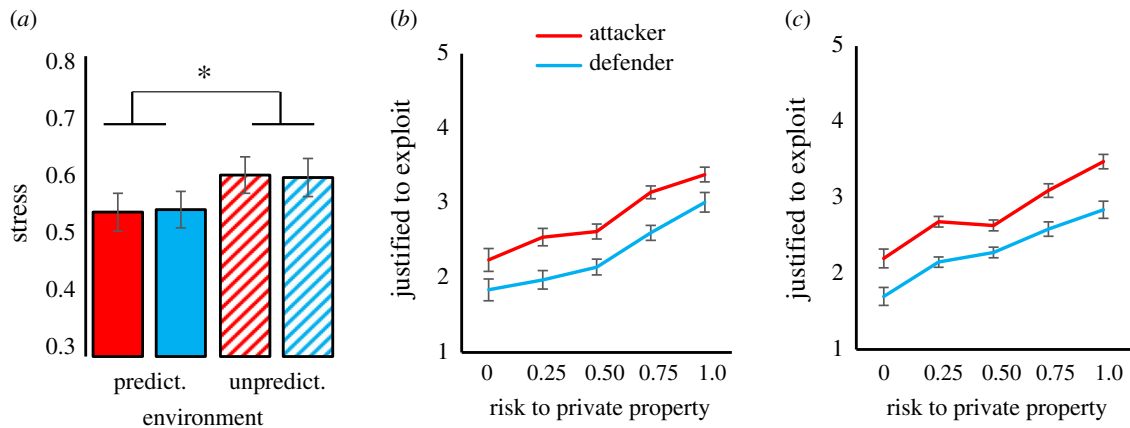


Figure 1. Psychological responses to unpredictable environments. (a) Reported stress when the attackers' (red bars) and defenders' (blue bars) environment is predictable (solid bars) versus unpredictable (dashed bars) (range -2 to $+2$; displayed $m \pm s.e.$); $*p \leq 0.05$ (Bonferroni-corrected). (b,c) Justifiability to exploit another group (1 = not at all, to 5 = very much) under different hypothetical probabilities of environmental unpredictability in Experiment 1 and a replication in Experiment 2 (displayed $m \pm s.e.$).

within-group solidarity and feelings of in-group (versus out-group) entitlements.

3. Experimental methods and results

Across experiments, we tested 157 male and 305 female subjects in total (mean age \pm s.d. = 21.67 ± 1.94). Sample sizes were set *a priori* to fit earlier intergroup contest and public good provision experiments [40,41,58]. For each IADC session, six subjects in individual cubicles were divided at random into a three-person attacker group and a three-person defender group. Since groups were randomly composed of male and female members, gender composition was considered a constant across experimental treatments and not further considered.

Instructions used neutral language throughout (e.g. groups were referred to as Group A and B, contributions were labelled 'investments', and terms like 'in-group defense' and 'out-group attack' were avoided). All subjects passed a comprehension check that consisted of two complete scenarios for one round of the IADC from the perspective of their role, with their group winning and losing the episode, respectively. Thereafter, subjects indicated their contribution g ($0 \leq g_i \leq 20$) to their group's pool C , and they were informed about the total contribution their group made to C ($0 \leq C \leq 60$), the total contribution C made by the other group, and the total earnings to the members of their own group, themselves included. This concluded one IADC investment round. An IADC session involved 40 (30) contest rounds between an attacker and its defender group in Experiment 1 (Experiment 2).

Experiment 1 had 210 subjects in 35 six-person attacker-defender contests. It compared the baseline IADC [58,59] to a treatment in which the personal endowments of the individuals in the attacker and/or defender group were at risk. In the baseline IADC, everything not invested in attack or defense is for the individual to keep and adds directly to their payment (in the role of defender, only when the group wins the contest). In the unpredictability treatment, individuals in each group faced a risk of destruction u of the non-invested individual endowment. Specifically, the endowment not invested was subject to a fixed probability of loss $u = 0.40$. When $u = 0$ (0.40), individuals keep

what they do not contribute with probability 1.0 (0.6). The unpredictability parameter u was announced before and implemented after each investment round and did not apply to attackers' earnings from the contest.

We created four blocks of 10 investment rounds each by orthogonally varying u (0.00 versus 0.40) for the attacker and defender group, resulting in a 2 (attackers' u : 0.40 versus 0.00) \times 2 (defenders' u : 0.40 versus 0.00) factorial design. The order in which blocks were presented was controlled in a Latin Square structure and did not influence results. After each 10-round block, subjects indicated how stressed, nervous, tense and worried they felt (all -2 = not at all, to $+2$ = very much). Ratings were averaged in one index for stress (Cronbach's $\alpha = 0.76$) (our data analytic strategy is described in §2 of the electronic supplementary material). Analysis confirmed that unpredictable environments were experienced as more stressful. Following contest blocks in which their group faced an unpredictable rather than predictable environment, participants reported more stress (figure 1a: attackers' environment: $F = 6.663$, $p = 0.015$; defenders' environment: $F = 4.702$, $p = 0.037$; electronic supplementary material, table S1). In addition, when responding to hypothetical scenarios in which private property was at various levels of risk, individuals felt that out-group exploitation was more justified especially when they were part of attacker groups (figure 1b,c; $F = 16.228$, $p < 0.001$).

In Experiment 1 individuals contributed, on average, less to out-group attack than to in-group defense and, in both cases, above the game-theoretic predictions (figure 2a,b). Individuals in defender groups mainly responded to their attackers' behaviour and environmental unpredictability had few effects on in-group defense (electronic supplementary material, tables S2–S4). Furthermore, environmental unpredictability increased out-of-equilibrium investments more in attackers ($m \pm s.e. = 2.415 \pm 0.442$ to $m \pm s.e. = 3.797 \pm 0.741$) than in defenders (from $m \pm s.e. = 3.515 \pm 0.544$ to $m = 3.678 \pm 0.363$) (paired $t = 2.850$, $p = 0.007$). Indeed, when attacker groups faced an unpredictable rather than a predictable environment, out-group attack increased substantially from $m \pm s.e. = 7.825 \pm 0.741$ to $m \pm s.e. = 11.035 \pm 0.544$ (attacker's environment \times role: $F = 40.762$, $p < 0.001$). This gives some first indication that carrying-capacity stress increases out-group attack in particular, and beyond what a game-theoretic

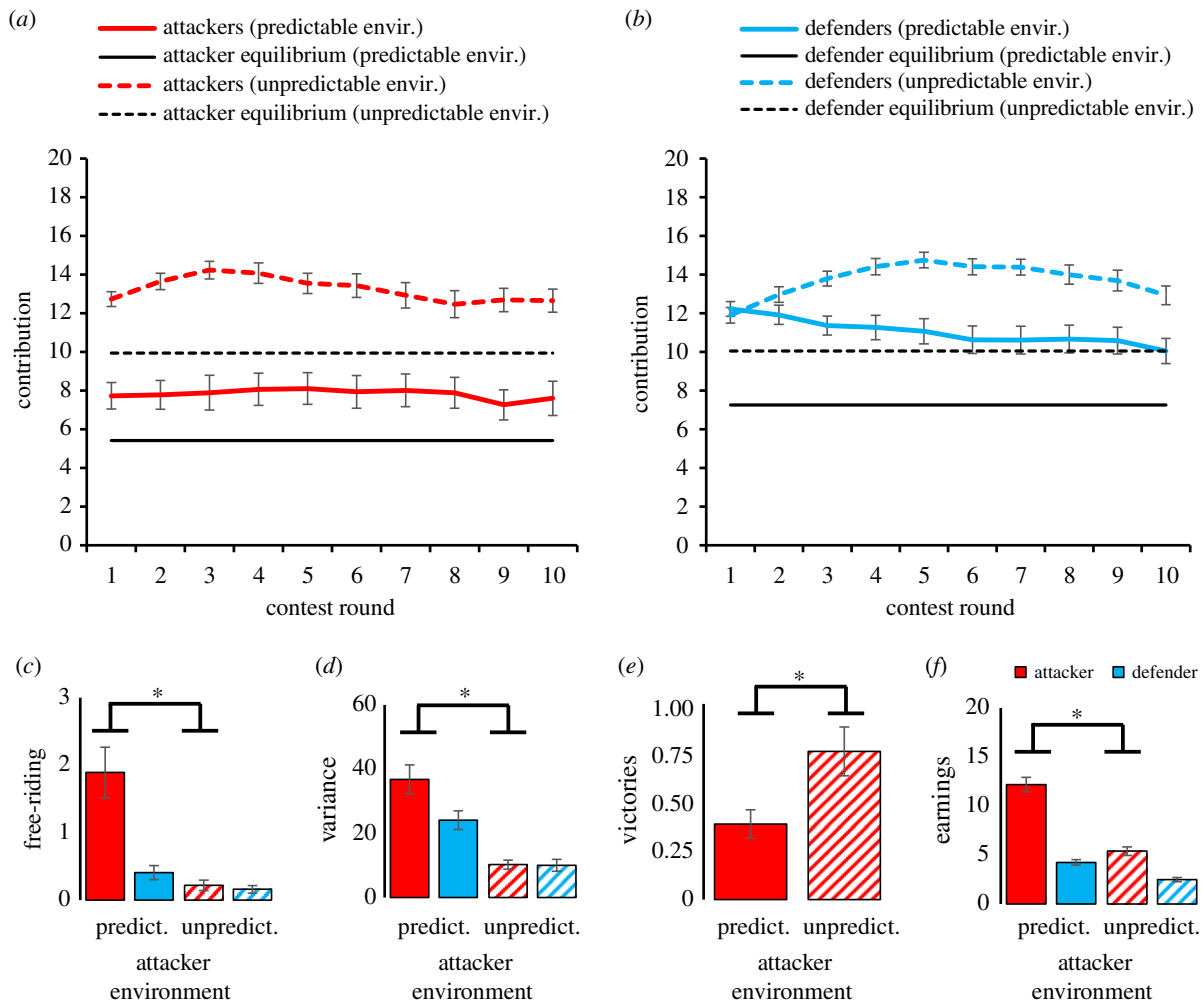


Figure 2. Intergroup conflict when attacker groups are under (un)predictable environments (collapsed across defender group's (un)predictability). (a) Contributions to out-group attack (range 0–20; displayed $m \pm s.e.$). (b) Contributions to in-group defense (range 0–20; displayed $m \pm s.e.$). (c) Free-riding within groups across contest rounds (range 0–3; displayed $m \pm s.e.$), $*p \leq 0.05$ (Bonferroni-corrected). (d) Within-group variance in contributions as a measure of group coordination; $*p \leq 0.05$ (Bonferroni-corrected). (e) Victory rates for out-group attacks (proportion out of 10 rounds). (f) Post-contest wealth (displayed $m \pm s.e.$), $*p \leq 0.05$ (Bonferroni-corrected).

analysis based on a shift of expected value of conflict would predict. Possibly, therefore, out-group attack is also motivated by additional psychological processes such as a heightened sense of in-group solidarity and considerations of entitlement.

Environmental unpredictability already influenced out-group attack early in the contest (figure 2*a,b*; attacker's environment \times role \times round, $F = 3.592$, $p = 0.005$) and independently of the defender's environmental (un)predictability (electronic supplementary material, tables S2–S4). On the first contest round, when groups were unaware of how others would behave and environmental unpredictability had not been effectuated, out-group attack was already stronger under environmental unpredictability ($F = 48.841$, $p < 0.001$; role \times attacker environment, $F = 41.417$, $p < 0.001$). Defense was not significantly influenced by environmental unpredictability ($F = 41.417$, $p = 0.652$; role \times defender environment, $F = 2.4179$, $p = 0.125$).

Analyses of within-group dynamics and individual decisions revealed further support for the possibility that environmental unpredictability increases parochialism especially during out-group attack. Individuals in attacker groups free-rode less frequently (i.e. investing 0 in the conflict) when their environment was unpredictable (figure 2*c*: attacker's environment \times role, $F = 22.127$, $p < 0.001$). Individuals in attacker groups facing unpredictable environments

also reduced within-group variance in contributions, suggesting improved coordination of collective action (figure 2*d*; attacker's environment \times role, $F = 7.959$, $p = 0.008$; electronic supplementary material, tables S3–S4). Hence, environmental unpredictability intensified intergroup conflict because it increased conflict participation and within-group coordination in attacker groups. Within-group coordination is difficult to explain from the perspective of expected value analysis, and results give further support to the possibility that carrying-capacity stress can lead to conflict (also) because it increases group cohesion and within-group solidarity.

Under unpredictable environments, out-group attacks were successful almost twice as frequently (from 39.2% to 75.8%; $F = 20.734$, $p < 0.0001$; figure 2*e*). Whereas attacker victory rate fits the game-theoretic equilibrium of 37.5% for predictable environments (one-sample $t = 0.148$, $p = 0.883$), it significantly exceeds the predicted 53.15% in unpredictable environments (one-sample $t = 1.988$, $p = 0.048$). At the same time, attacker groups exposed to unpredictable environments earned significantly less than those operating under predictable conditions (figure 2*f*; attackers' environment \times role; $F = 144.789$, $p < 0.001$; electronic supplementary material, tables S3–S4). Thus, while groups react to unpredictability by

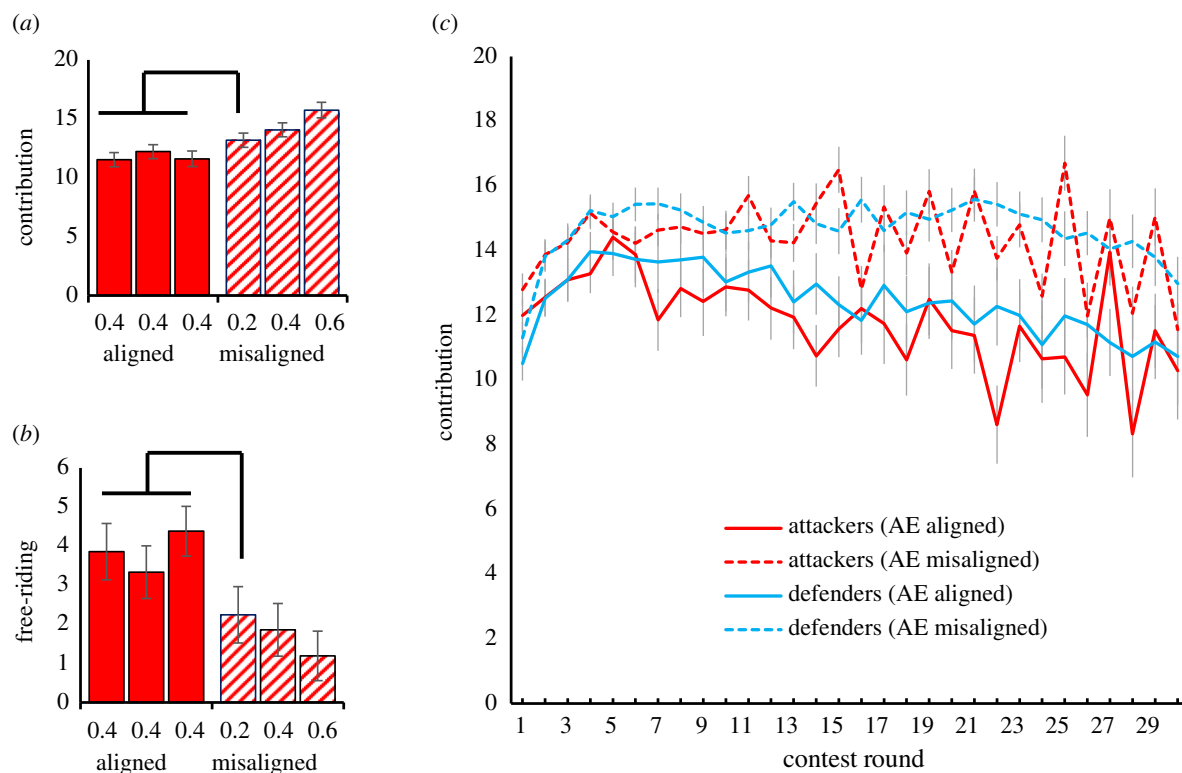


Figure 3. Group dynamics in attacker groups when they face aligned versus misaligned environmental unpredictability (AE), with all members in the aligned condition being at round 1 under $u = 0.4$, and in the misaligned conditions being at $u = 0.2$ versus 0.4 versus 0.6 . (a) Average individual contributions (range 0–20; displayed $m \pm s.e.$). (b) Free-riding per individual across contest rounds (range 0–30; displayed $m \pm s.e.$); bars linked with connectors are significantly different at Bonferroni-corrected $p \leq 0.05$. (c) Contributions to out-group attack and in-group defense over time (range 0–20; displayed $m \pm s.e.$).

intensifying their attempts to take advantage of another group, they end up less wealthy. Furthermore, environmental unpredictability reduces relative wealth differences between attacker and defender groups—environmental unpredictability makes groups not only aggressive and victorious, but also poor.

Results for earnings and victory rates suggest that out-group aggression triggered by unpredictable environments is maladaptive from a (within-group) welfare perspective yet adaptive from a relative gain perspective—it makes groups more frequently victorious. Perhaps unpredictable environments and ensuing carrying-capacity stress shift the group members' goal from maximizing wealth to maximizing winning. This resonates with studies showing that stress due to cognitive load and time pressure lead to more aggressive attacks and lower earnings, yet higher victory-rates [54]. Furthermore, such a 'glow of winning' is associated with activation in brain regions related to value computation (i.e. ventral striatum) [62] and reduced activation in brain regions typically associated with controlled cost–benefit analysis and impulse inhibition (i.e. dorsolateral prefrontal cortex) [59].

A possible concern with Experiment 1 is that all members in one group faced the same level of unpredictability. This shared common fate may in itself create and increase group cohesion [35–38]. Accordingly, it may be shared common fate rather than unpredictable environments that led to increased parochialism and out-group aggression. We examined this possibility in Experiment 2, with 252 subjects in 42 contests. Methods and materials were identical to those in Experiment 1, with a few exceptions. Defender groups were always under $u = 0$ and attacker groups were always under $u = 0.40$ on average. Second, environmental unpredictability u was conditional on contest success: if an attacker group

won (lost) a contest round, each member's u decreased (increased) with 0.05 (until u plateaued at 0 or 1). However, because victory rate (49.3%) did not change across the contest ($F = 1.148$, $p = 0.417$), attacker groups mostly maintained a stationary environmental unpredictability at $u \approx 0.40$ and this element in the experiment is subsequently ignored (electronic supplementary material, table S5).

We decomposed a shared common fate and an environmental unpredictability explanation by manipulating, within attacker groups, the individual's personal risk of destruction. In 21 attacker groups, environmental unpredictability was the same for each group member ($u = 0.40$). In another 21 attacker groups, unpredictability differed across group members: One member of an attacker group was under $u = 0.20$, one was exposed to $u = 0.40$, and the third group member was exposed to $u = 0.60$. If shared common-fate rather than environmental unpredictability explains the results of Experiment 1, we should see stronger parochialism in attacker groups with aligned (i.e. $u = [0.4, 0.4, 0.4]$) compared to misaligned (i.e. $u = [0.2, 0.4, 0.6]$) risk to private property.

Results do not support the common fate explanation: out-group attack was higher on average when environmental unpredictability was misaligned rather than aligned ([mis]alignment $F = 12.429$, $p = 0.001$; member \times [mis]alignment: $F = 5.462$, $p = 0.006$; figure 3a) (electronic supplementary material, tables S7 and S8). Crucially, individuals in the misaligned condition with lower unpredictability (i.e. $u = 0.20$) contributed more to out-group attack than individuals in the aligned condition (facing higher unpredictability, i.e. $u = 0.40$; figure 3a). The same pattern was observed for free-riding, which was lower under misaligned environmental unpredictability ($F = 6.308$, $p = 0.016$) and lower among individuals with low

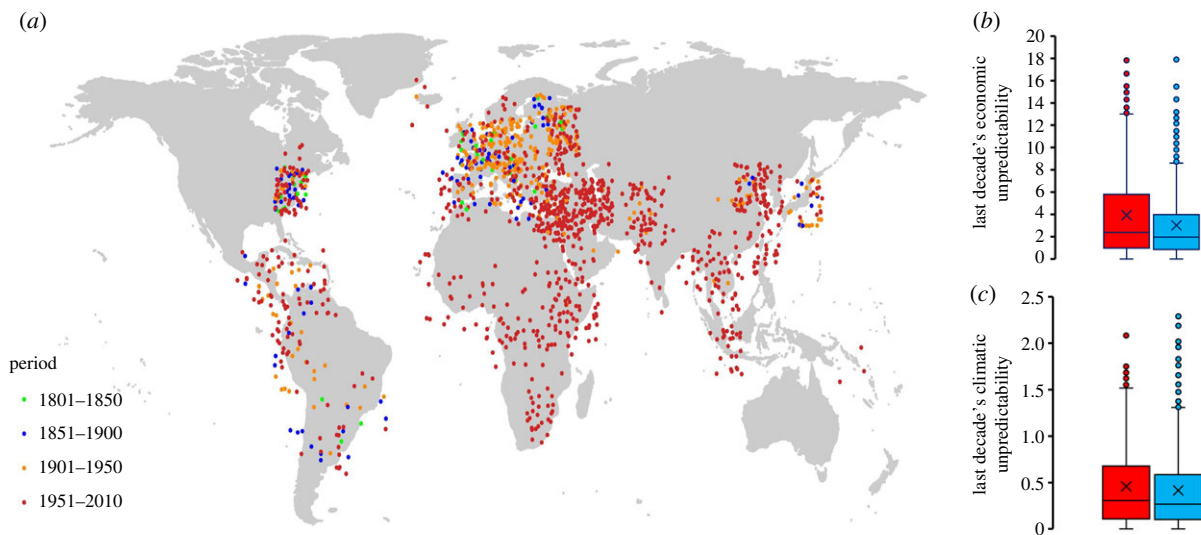


Figure 4. World map with 1,474 interstate disputes showing revisionist aggressors (dots, jittered per country) and their non-revisionist defenders (green = 1800–1851; blue = 1851–1900; orange = 1901–1950; red = 1951–2010). In the decade prior to conflict onset, revisionist aggressors (red bars) faced greater fluctuations in *per capita* economic productivity (b) and in annual surface temperature (c) than their non-revisionist ‘defenders’ (blue bars). (Box-plots based on (b) 1427 and (c) 1053 conflict pairs, respectively, with whiskers showing standard deviation around the mean [×] and median (horizontal bars within the boxes).)

unpredictability in the misaligned condition ($u = 0.20$) than those with higher unpredictability ($u = 0.40$) in the aligned condition (figure 3b: member × [mis]alignment: $F = 2.996$, $p = 0.091$; marginal). Hence, individuals in the misaligned condition facing lower risks ‘stood by’ their group members facing higher risks. Such a display of within-group solidarity is difficult to explain from an expected value perspective. It fits, however, the hypothesis that unpredictable environments increase parochialism and intergroup conflict, even for those individuals that are less affected [8,63].

At the aggregate level, we replicated Experiment 1. Contributions were lower in attacker compared to defender groups ($F = 12.071$, $p = 0.001$), and both attack and defense were out-of-equilibrium. Furthermore, we found that contributions to out-group attack were higher when environmental unpredictability was misaligned ($F = 11.856$, $p = 0.001$; figure 3c). Under aligned unpredictability, attack intensified early on and then steadily declined. When unpredictability was misaligned, however, contributions to attack increased and then stabilized (round × [mis]alignment: $F = 2.720$, $p = 0.035$; electronic supplementary material, tables S7 and S8).

4. Archival analysis of interstate conflict

At the outset, we noted that archival and macroeconomic data documented that environmental shocks link to nationalistic sentiments [43,49–52,64] and that nationalism links to hawkish foreign policy [10,51,64]. Our experiments reveal the possible micro-foundations of such macrolevel tendencies by showing how environmental unpredictability and concomitant carrying-capacity stress strengthens within-group solidarity and the ability to align behaviour in well-coordinated collective action. Possibly, carrying-capacity stress also promotes the formation of and compliance with in-group norms and leader initiatives aimed at aggressing neighbouring communities and nation states [38,65]. Local sentiments and parochial interests among groups and communities within an overarching nation state may support and fuel nationalism and support for hawkish foreign policy [10,31,60,64–67]. If true, we

should see that environmental unpredictability and ensuing carrying-capacity stress associates with enhanced probability of nations aggressing their neighbours more than with nations defending against their neighbour’s aggression. We examined this possibility in archival analyses of 1447 militarized disputes [58,60,61] between revisionist ‘aggressor’ states and their non-revisionist ‘defenders’ (figure 4a; electronic supplementary material §III).

We first looked at environmental unpredictability in terms of economic productivity. For each country within 1053 aggressor–defender pairs we created *per capita* economic productivity growth vectors for the ten years prior to the onset of the dispute [68,69] (electronic supplementary material §III). Each value within each country’s 10-year series was expressed as the percentage deviation from the 10-year mean. We fitted regression lines to these adjusted values and used the residual standard deviation to index economic variability. Fitting the micro-level dynamics uncovered in our experiments, we find that in the decade prior to conflict onset, aggressors compared to their defenders experienced higher economic variability ($b \pm se = 0.6547 \pm 0.1543$, $p < 0.001$; figure 4b). Next we considered environmental unpredictability in terms of climatic variability. For 1427 aggressor–defender pairs, we obtained the hemispheric coordinates of each country’s capital city at the onset of the conflict [70] and matching 10-year annual surface temperature vectors [71] (electronic supplementary material §II). We fitted linear regression models to each 10-year temperature vector within each country and took the residual standard deviation as a measure of climatic variability. We find that in the decade prior to conflict onset, aggressors compared to their defenders experienced more climatic variability ($b \pm se = 0.093 \pm 0.016$, $p < 0.001$; figure 4c; electronic supplementary material, tables S9–S11).

5. Conclusion

The results of our experiments taken together show that when risk to private property is shared with other group

members, individuals feel stressed and justified to extract resources from another group. When environmental unpredictability increased, individuals contributed more to their group's efforts to exploit other groups through coordinated out-group attacks and were more victorious. These effects of unpredictable environments on out-group attacks emerged already in the first round of the intergroup contest (figures 1a and 4c; electronic supplementary material, tables S3 and S7A). At this point in the contest, the strength of defense is unknown and environmental unpredictability has not been effectuated. This suggests that groups respond to unpredictable environments preemptively by initiating conflict with another group.

To some extent, group members may be more motivated to contribute resources to intergroup conflict when the environment is unpredictable as the expected value of private property is reduced. This possibility fits game-theoretic predictions. Importantly, however, we observed significant over-investment compared to risk-neutral rational selfish play, especially for out-group attack. That contributions and attacker victory rates were persistently out-of-equilibrium reveals that rational selfish play cannot fully explain results when the environment is either predictable or unpredictable. Instead, results fit earlier work suggesting that the stress induced by environmental unpredictability focuses investments towards group winning rather than individual or group-level profit-maximization [54,57,59]. Results showed that at the group level, environmental unpredictability strengthens within-group solidarity and effective coordination of collective action aimed at exploiting rivaling out-groups.

Groups respond to unpredictable environments by fighting other groups, both in laboratory experiments and at the interstate level. While the 'spoils of war' from victories and the 'glow of winning' may provide some immediate reward, our results suggest that unpredictable environments lead to out-group attack and in-group defense that substantially reduce individual welfare and collective efficiency. In our experiments, groups facing predictable environments wasted 53% of their collective resource on intergroup conflict. When the environment became unpredictable, waste increased to 82% (and 75% in Experiment 2).

Our experimental set-up allowed individual group members to contribute either to out-group attacks or to in-group defense. There are situations in which individuals can do both to varying degrees, or in an alternating fashion between defending and attacking. Even within groups, some may contribute resources to in-group defense while others contribute to out-group attack. Our experiments teased apart out-group attack and in-group defense to cleanly estimate the possible impact of environmental unpredictability and concomitant carrying-capacity stress. It allows us to conclude that changes in the group's environment condition out-group aggression more than in-group defense. Future research could examine this conclusion when individuals are able to contribute to

both defense and attack. In addition, our experimental set-up allowed groups no other means to serve group welfare than to attack out-groups. Peaceful solutions to unpredictable environments would mean that groups refrain from investing in out-group attack and collectively 'free-ride' during the contest. Alternative solutions, including investing in local group goods and innovation, are sometimes available as well. Future studies could examine environments that allow groups under varying levels of environmental unpredictability to choose between peaceful and aggressive options to serve their group. There is some evidence that group innovation in science and technology increases under harsher, more unpredictable environments [72] but whether and to what extent possibilities for group innovation reduce out-group attack and intergroup conflict as a response to unpredictable environments remains an open question.

Conflict theory and research in the social and behavioural sciences explain the prevalence and re-occurrence of conflict between human groups and societies mainly in terms of elements inherent to and endogenously created by histories of competitive intergroup exchanges [4–16]. Consistent with recent work in political geography and climate science [17–22], and on intergroup conflict among non-human animals [23–25], we identified here when and how ecological risks, and changes therein, can lead humans to contribute to out-group aggression. While pro-social inclinations to reduce the in-group's carrying-capacity stress may motivate such out-group aggression, it turns potentially benign intergroup relations into inherently wasteful conflict.

Ethics. Experiments were approved by the Psychology Research Ethics Board of Leiden University (file CEP17-0909/289). Subjects provided written informed consent and were debriefed. The experiments involved no deception and subjects received a €6.50 show-up fee and $M = €3.86$ (range 0–€10) for their performance during four randomly selected contest rounds.

Data accessibility. All data and computing scripts are deposited in DataVerse <https://doi.org/10.34894/HZD5NV>.

Full analytic models and results are provided in electronic supplementary material [73].

Authors' contributions. C.K.W.D.D. and J.G. conceived of the project and designed the studies. J.G. and C.K.W.D.D. performed experiments and L.R. performed archival analyses. C.K.W.D.D. and L.R. analysed data. C.K.W.D.D. wrote the paper and incorporated co-author inputs and revisions.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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