Accurate Prediction of Antibody Resistance in Clinical HIV-1 Isolates

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Broadly neutralizing antibodies (bNAbs) targeting the HIV-1 envelope glycoprotein (Env) have promising utility in prevention and treatment of HIV-1 infection with several undergoing clinical trials. Due to high sequence diversity and mutation rate of HIV-1, viral isolates are often resistant to particular bNAbs. Resistant strains are commonly identified by time-consuming and expensive *in vitro* neutralization experiments. Here, we developed machine learning-based classifiers that accurately predict resistance of HIV-1 strains to 33 neutralizing antibodies. Notably, our classifiers achieved an overall prediction accuracy of 96% for 212 clinical isolates from patients enrolled in four different clinical trials. Moreover, use of the tree-based machine learning method gradient boosting machine enabled us to identify critical epitope features that distinguish between antibody resistance and sensitivity. The availability of an *in silico* antibody resistance predictor will facilitate informed decisions of antibody usage in clinical settings.

Introduction

During the past decade, broadly neutralizing antibodies (bNAbs) were isolated from sera of HIV-1 chronically infected donors, with several undergoing clinical trials for use of preventing and treating HIV-1 infection (1-3). As a result of the high sequence diversity and mutation rate of HIV-1, HIV-1 viral isolates can be resistant to a particular bNAb and administration of bNAbs may lead to viral escape (Figure 1a). Resistant viral strains are usually identified by subcloning or synthesizing amplified Envs, producing pseudoviruses, and performing *in vitro* neutralization assays (1), which is time-consuming and expensive.

While many genotypic assays and *in silico* algorithms have been developed to predict HIV-1 drug resistance (4) and co-receptor usage (5), *in silico* prediction of neutralization susceptibility to bNAbs has only been explored by a few studies (6-8), none with publicly available software.

In this work, we present bNAb-Resistance Predictor (bNAb-ReP), an HIV-1 isolate antibody resistance predictor based on the white-box non-linear predictive modeling technique, gradient boosting machine (GBM) (Supplementary Figure S1). GBM has been shown to be competitive with black-box non-linear modeling techniques such as deep learning, particularly when large amounts of training data are not available (9, 10). To build bNAb-ReP, we used sequence and neutralization data for 33 HIV-1 bNAbs obtained from the CATNAP database (11). Full Env sequences and IC_{50} neutralization titers for 205 to 711 HIV-1 isolates with varying clade distributions were available for each bNAb (Supplementary Figure S2).

Results and discussion

The performance of bNAb-ReP was evaluated in ten runs of ten-fold cross validation measured as the area under the receiver operating characteristic curve (AUC). All bNAb-ReP classifiers performed better than random prediction with average AUC values between 0.63 and 0.97 and an overall median AUC of 0.83 (Figure 1b). Notably, the AUC scores were significantly higher in 26 of the 33 cases using GBM when compared to conventional prediction methods like logistic regression and random forest (Supplementary Figure S3).

In contrast to black-box machine learning approaches, the major advantage of the tree-based method, GBM, is the ability to obtain variable importance scores for all input features,

which enables interpretability of the predictive models (feature importance for all 33 bNAb classifiers can be found under https://github.com/RedaRawi/bNAb-ReP). For instance, the top three discriminative features of the bNAb VRC01 classifier involve HIV-1 Env residues 414A, 456, and 459 with a total feature importance of 24.84% (Figure 1c, Supplementary Table S1). Structural studies revealed two of the three amino acid positions were located at the VRC01 epitope and thus can be critical to VRC01 binding and neutralization (Figure 1c) (12). Additionally, the top three features of bNAb 8ANC195 classifier account for a total variable importance of 48.47% and include Env residues 234 and 276, which must be glycosylated in order for 8ANC195 to bind and neutralize Env (Figure 1d, Supplementary Table S2) (13). Not all of the top discriminative features, however, involved bNAb epitope residues, suggesting that distal regions outside the epitope also affect neutralization susceptibility of HIV-1 strains (Supplementary Table S4). In particular, the prediction accuracy for glycan-V3 directed bNAbs had the highest reduction when using only epitope regions rather than full Env sequences. These feature importance scores provide helpful information to facilitate bNAb optimization and guide immunogen design.

To validate bNAb-ReP beyond the data sets obtained from CATNAP, we predicted antibody resistance of HIV-1 Env sequences from clinical studies of HIV infection. First, we tested the bNAb VRC01 classifier on clinical HIV-1 isolates obtained from HIV positive patients enrolled in the VRC601 trial (1) studying the efficacy of VRC01 as therapeutic to control viral load. bNAb-ReP correctly predicted 100% of the resistant and 87% of the sensitive strains to VRC01 (Figure 2a, b).

Additionally, we evaluated the prediction performance of bNAb-ReP using sequence and neutralization data from a phase IIa clinical trial studying HIV positive patients treated

with bNAb 3BNC117 (3). bNAb-ReP's overall classification accuracy was 87%, correctly predicting 26 of 29 sensitive HIV-1 Env strains, although falsely predicting the only resistant sequence as sensitive (Supplementary Figure S5).

To further evaluate bNAb-ReP's prediction accuracy, we performed *in vitro* neutralization assay experiments on clinical sequences obtained from Bar et al. (Supplementary Data S1 and Table S4) (2). bNAb-ReP predicted neutralization susceptibility to VRC01, 3BNC117, 10-1074, and PGT121 with accuracies of 82%, 96%, 100%, and 100%, respectively (Figure 2c).

In addition to predicting neutralization susceptibility from the aforementioned clade B sequences, we used bNAb-ReP to predict resistance for clade A and A/D recombinant sequences from a superinfection case study in a Ugandan couple (14). Interestingly, the bNAb-ReP classification accuracy was 100%, 93%, 100%, 100%, 100%, and 100%, for bNAbs VRC01, PGT121, PGT128, PGT145, VRC26.25, and VRC34.01, respectively (Figure 2e).

In this work, we developed bNAb-ReP, a GBM-based antibody resistance predictor, and demonstrated bNAb-ReP's ability to predict neutralization susceptibility of HIV-1 isolates with high accuracy for several independent clinical test sets. The underlying machine learning technique, GBM, provided insight into how specific features can distinguish between predicting resistance and sensitivity in HIV-1 strains, informing antibody optimization and immunogen design experiments. The availability of bNAb-ReP will facilitate easy and fast prediction of HIV-1 isolates for their neutralization susceptibility to bNAbs, allowing real-time assessment in a clinical setting. The bNAb-ReP predictors for 33 HIV-1 bNAbs are available for download at https://github.com/RedaRawi/bNAb-ReP.

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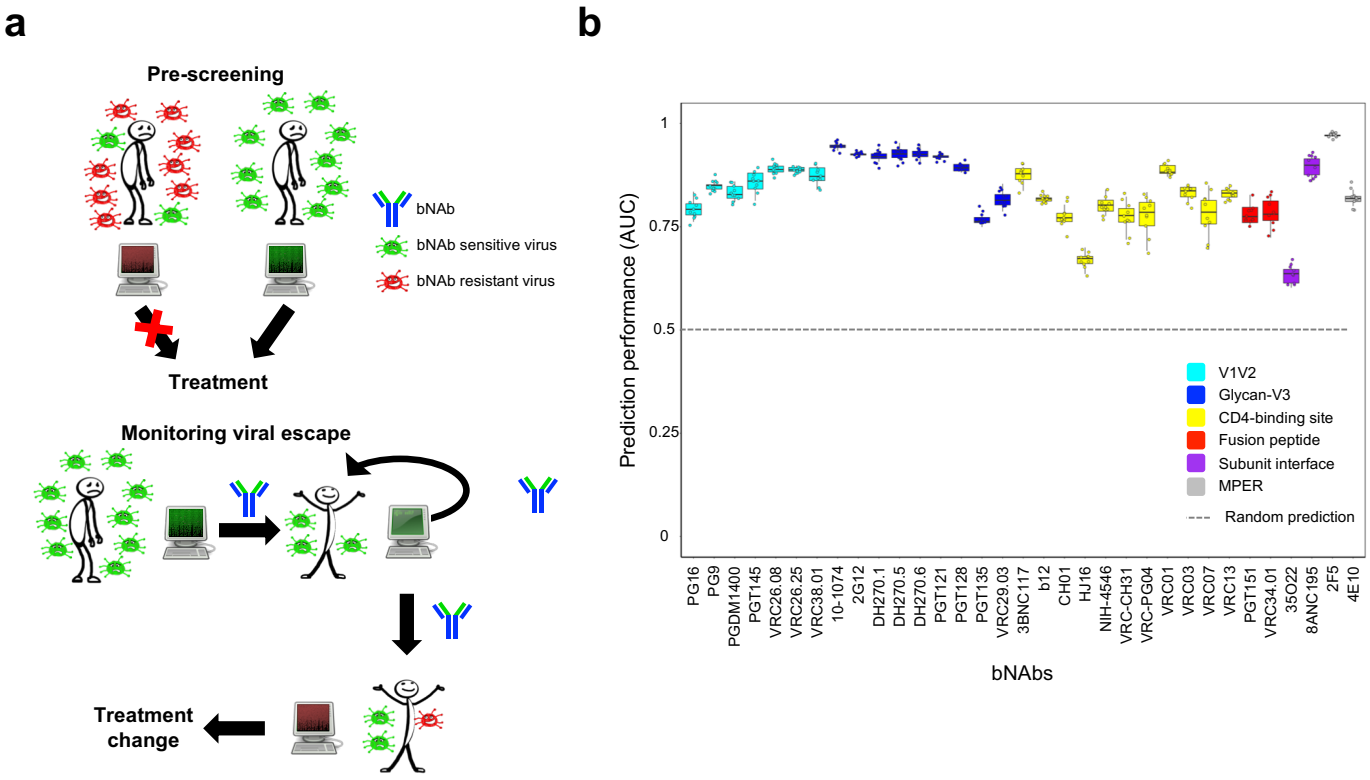

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	Feature	Position	Importance (%)	P-value	Odds ratio	Classification
1	Residue: Gly	459	11.14	< 0.0001	0.05	Sensitive
2	Residue: Arg	456	9.02	< 0.0001	0.03	Sensitive
3	Residue: Ile	414A	4.68	< 0.0001	12.48	Resistant

d

	Feature	Position	Importance (%)	P-value	Odds ratio	Classification
1	Residue: Glycan	234	22.88	< 0.0001	0.02	Sensitive
2	Residue: Asn	234	13.39	< 0.0001	59.97	Resistant
3	Residue: Glycan	276	12.20	< 0.0001	0.06	Sensitive

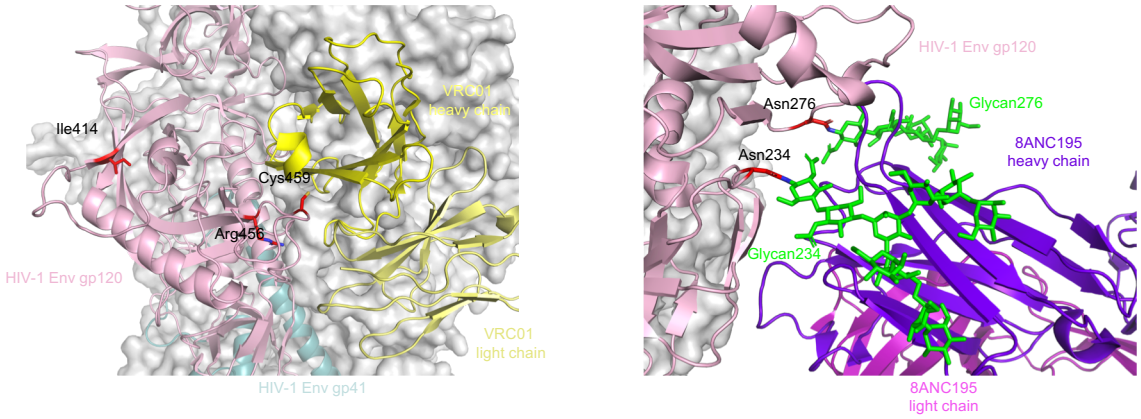

Figure 1. Prediction performance and feature importance of the bNAb-ReP classifiers
(**a**) Schematics illustrating potential applications of bNAb-ReP. (**b**) Prediction performance (AUC) of 33 bNAb classifiers determined by ten runs of ten-fold cross-validation, color-coded based on epitope category. (**c**) The top three discriminant features of the bNAb VRC01 classifier are listed in the table and highlighted on the prefusion-closed Env trimer structure in complex with VRC01 antibody (PDB ID: 5FYJ). (**d**) The top three discriminant features of the bNAb 8ANC195 classifier are listed in the table and highlighted in the Env trimer structure in complex with 8ANC195 bNAb, with glycans 234 and 276 depicted as green sticks (PDB ID: 5CJX).

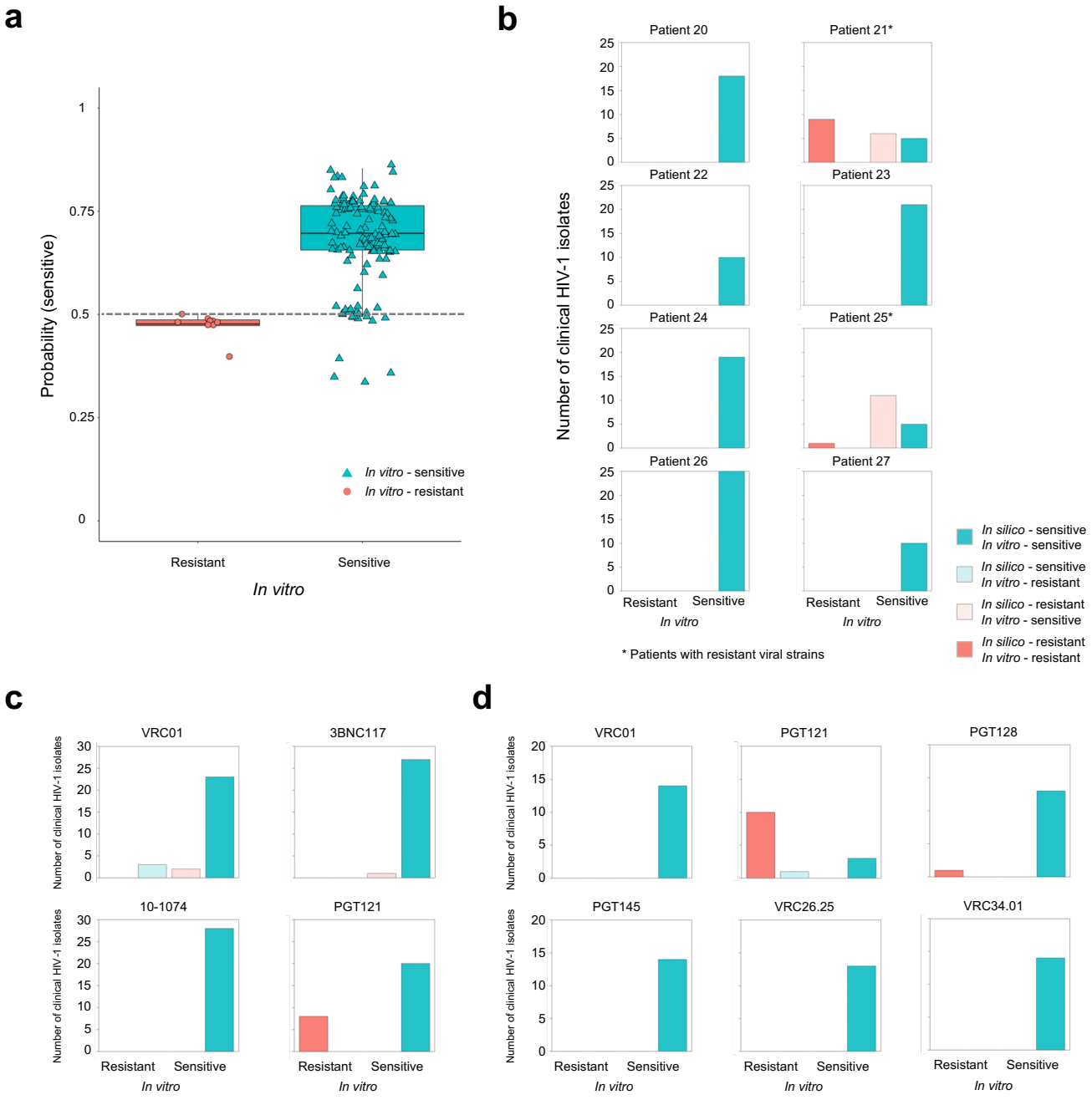

Figure 2. bNAb-ReP prediction performance on clinical HIV-1 isolates
(**a**) Prediction performance of the susceptibility of VRC601 clinical isolates to VRC01. *In vitro* assay neutralization classification is shown on the x-axis, with the *in silico* predicted probability for a sequence to be sensitive to VRC01 shown on the y-axis. The classification cutoff of 0.5 is depicted with a grey dashed line. (**b**) Bar plots depicting the number of *in vitro* classified VRC601 HIV-1 isolates per patient. Clinical HIV-1 isolates *in silico* predictions are shown in red (resistant) and cyan (sensitive) with darker colors indicating true predictions and light colors indicating false predictions.(**c**) Bar plots highlighting the number of clinical HIV-1 isolates, introduced in the Bar et al. study, separated according to their *in silico* predictions. Resistant *in silico* predictions for bNAbs VRC01, 3BNC117, 10-1074, and PGT121 are shown in red and sensitive in cyan, with darker colors representing accurate predictions and light colors inaccurate ones, respectively. (**d**) Bar plots depicting the number of isolates, introduced by Ssemwanga et al., with resistant *in silico* predictions shown in red and sensitive in cyan.

Materials and methods

Training data

We used neutralization data of 33 different antibodies (10-1074, 2F5, 2G12, 35O22, 3BNC117, 4E10, 8ANC195, CH01, DH270.1, DH270.5, DH270.6, HJ16, NIH-4546, PG16, PG9, PGDM1400, PGT121, PGT128, PGT135, PGT145, PGT151, VRC-CH31, VRC-PG04, VRC01, VRC03, VRC07, VRC13, VRC26.08, VRC26.25, VRC29.03, VRC34.01, VRC38.01 and b12) assayed against 205 to 711 HIV-1 isolates published in the CATNAP database (1). These assays were performed using single-round-of-infection Env-pseudoviruses on cell lines (2, 3). Each HIV-1 isolate is represented with its full-length envelope glycoprotein amino acid sequence. Duplicated full-length HIV-1 envelope sequences were removed. The viral isolate was categorized as resistant to an antibody if its geometric mean IC_{50} is greater than 50μg/ml or designated with a ">" sign or was categorized as sensitive otherwise.

Test data

For the data from VRC601 clinical trial, we used sequences and neutralization data from Env-pseudoviruses generated from Envs isolated by single genome amplification (SGA) RT-PCR from plasma virus, as described in Lynch et al. (4). The Env-pseudoviruses were assayed on TZM-bl cells as in Sarzotti-Kelsoe et al. (3). The clade A and A/D sequences and neutralization data were generated the same way and were taken from Ssemwanga et al. (5). The VRC01-ATI sequences were derived from patients in an analytical treatment interruption trial, in which volunteers based at the NIH were administered VRC01 infusions before and during an interruption of antiretroviral therapy (6). In that publication, Env sequences were generated by SGA; however, the published neutralization assays were performed with infectious virus from outgrowth cultures, not in the Env-pseudovirus/TZM-bl format. Here, we report new data, for which we expressed the Env-pseudoviruses from the sequences reported in Bar et al. and used the TZM-bl format as above (6).

Gradient boosting machine (GBM)

To build the training models, we employed a non-linear interpretable tree-based ensemble technique referred as gradient boosting machine (GBM) for building antibody resistance predictors using *h2o* package (Version 3.16.0.2) in *R* software (https://www.R-project.org) (7, 8). GBM belongs to the family of predictive methods, which uses an iterative strategy such that the learning framework will consecutively fit new models so as to have a more accurate estimate of the response variable after each iteration. The primary notion behind this technique is to construct new tree-based learners to be as correlated as possible with the negative gradient of a given loss function, calculated using all the training data. We can use any arbitrary loss function ($L(\cdot,\cdot)$) here. However, if the loss function is the most commonly used squared-loss

function, the learning procedure would result in consecutive residual error-fitting. Algorithm 1 summarizes the generic GBM approach.

Algorithm 1: Gradient Boosting Machine

- Input: $D = \{X_i, Y_i\}_{i=1\ to\ N}$, a differentiable loss function $L(Y, F(X))$ and the number of iterations A.
- Initial model: $F_0(X) = argmin_\gamma \sum_{i=1}^{N} L(Y_i, \gamma)$
    - For $a = 1\ to\ A$ do:
        - Compute the *pseudo-residuals*:
            - $p_i{}^a = -\left[\frac{\partial L(Y_i, F(X_i))}{\partial F(X_i)}\right]_{F(X) = F_{a-1}(X)}, \forall i = 1, \ldots, N$.
        - Fit a new base learner $\theta_a(X)$on the revised dataset $\{X_i, p_i{}^a\}_{i=1}{}^N$.
        - Compute the parameters $\rho_a$by solving the line-search problem:
            - $\rho_a = argmin_\rho \sum_{i=1}^{N} L(Y_i, F_{a-1}(X) + \rho_a \theta_a(X))$
        - Update the model: $F_a(X) = F_{a-1}(X) + \rho_a \theta_a(X)$

- Output: $F_a(X)$

The advantage of the boosting procedure is that it works on decreasing the bias of the model, without increasing the variance. Learning uncorrelated base learners helps to reduce the bias of the final ensemble model. In this work, we used the L_2- TreeBoost approach proposed in (7) to build the core GBM model. Here the loss function is the classical squared-loss function (L_2):

$$L_2 = \frac{1}{2} || Y - F(X) ||_2{}^2, Y \in \{0,1\}.$$

In our approach, the base learner is a J-terminal node classification tree. Each tree model has an additive form given as:

$$\theta(X; \{\gamma_j, P_j\})_{j=1}{}^J = \sum_{j=1}^{J} \gamma_j 1(X \in P_j).$$

Here $\{P_j\}_1{}^J$are J disjoint regions that together cover the space of all joint values of the predictor variable X. These regions represent the J terminal nodes of the corresponding classification tree. The indicator function $1(\cdot)$ takes the value 1 if the argument passed to it is true, and 0 otherwise. Because the regions are disjoint, $\theta(X)$ is equivalent to the prediction rule: $if\ X \in P_j\ , then\ \theta(X) = \gamma_j$. Now, the pseudo-residuals become:

$$p_i{}^a = -\left[\frac{\partial L_2(Y_i, F(X_i))}{\partial F(X_i)}\right]_{F(X) = F_{a-1}(X)} = Y_i - F_{a-1}(X_i), \forall i = 1, \ldots, N$$

The line search becomes:

$$\rho_a = argmin_\rho \sum_{i=1}^{N} ||Y_i - F_{a-1}(X_i) - \rho_a \theta_a(X_i)||_2{}^2$$

$$= argmin_\rho \sum_{i=1}^{N} || p_i{}^a - \rho_a \theta_a(X_i)||_2{}^2$$

Using classification trees as base learners, we use the idea of separate updates for each terminal region $P_j{}^a$ as proposed in (7) to get:

$$\rho_j{}^a = mean_{X_i \in P_j{}^a} (\gamma_j{}^a \, p_i{}^a) \quad (1)$$

The L_2- TreeBoost approach for two-class GBM is summarized in Algorithm 2.

Algorithm 2: L_2- TreeBoost method for GBM

- Input: $D = \{X_i, Y_i\}_{i=1 \; to \; N}$, and the number of iterations A.
- Initial model: $F_0(X) = mean\{Y_i\}_{i=1 \; to \; N}$
    - For $a = 1 \; to \; A$ do:
        - Compute the *pseudo-residuals*:
            - $p_i{}^a = Y_i - F_{a-1}(X_i), \forall i = 1, \ldots, N.$
        - $\{P_j{}^a\}_1{}^J =$ J-terminal node classification $tree(\{p_i{}^a, X_i\}_1{}^N)$.
        - Compute the parameters $\rho_j{}^a$ using Equation (1).
        - Update the model: $F_a(X) = F_{a-1}(X) + \eta \sum_{j=1}^{J} \rho_j{}^a \, 1(X \in P_j{}^a)$
- Output: $F_a(X)$

Here the parameter η is a regularization parameter which is used to avoid overfitting the models and is acquired via cross validation. For each iteration a, the least-squares criterion ($I(\phi)$) used to assess potential splits of a current terminal region P into two disjoint sub-regions (P_l, P_r) is given by:

$$i^2(P_l, P_r) = I(\phi) = \frac{w_l w_r}{w_l + w_r}(Y_l - Y_r)^2, \quad (2)$$

where Y_l and Y_r are the left and right child node responses respectively, and w_l, w_r are proportional to the number of samples in regions P_l and P_r respectively as show in (Friedman, 2001). $I(\phi)$ is a measure of the importance of the variable (ϕ) which maximizes this criterion. During a given iteration, only one feature is allowed to cause a split into 2 terminal regions. Thus, in the case of a J-terminal node classification tree, we generate $J - 1$ such measures. However, the same feature can generate multiple optimal splits for the J-terminal node tree. In such a scenario, we sum the importance of such features to get the total importance of each feature ϕ after A iterations. This procedure results in the variable importance scores from the GBM approach.

Classifier features

Sequence information was represented using one-hot encoding to represent 20 standard amino acids and N-linked glycan. Each amino acid aa_i, $i\epsilon\{1, \ldots, 21\}$ was translated into a 21-dimensional vector, where the i^{th} vector position was set to 1, and all other 20 vector positions were set to 0. For instance, applying one-hot encoding to an amino acid sequence of length 100, would be translated into a binary vector of length 2100.

Training of bNAb-ReP

To train bNAb-ReP classifiers, we first performed a hyperparameter optimization to identify the optimal GBM parameters for the given data. We created a grid of $T \times J \times r \times \eta = 120$, in particular number of trees $T = 1000$, maximum depth $J\epsilon\{1,2,3,4,5,6\}$, sample rate $r\epsilon\left\{\frac{\sqrt{\#features}}{\#features}, 0.1,0.2,0.3\right\}$, and learn rate $\eta\epsilon\{0.001,0.01,0.05,0.1,0.2\}$. We then performed ten-fold cross validation for each of the combinations. Finally, we selected the best parameters that had the maximal ten-fold cross validation area-under-the-curve (AUC). Once the optimal hyper-parameters are known, the model is built on the full training set using these parameters and its prediction performance is evaluated on the independent test set.

Alternative Predictors Logistic Regression and Random Forest

Logistic Regression belongs to the class of generalized linear models and we trained binomial predictors using *glm* function available in *h2o* package in *R*. Random Forest (RF) belongs to the class of ensemble based supervised white-box learning techniques. The RF algorithm applies the general technique of bagging or bootstrapped aggregating to decision tree learners. We performed a grid search for optimizing the hyper-parameters including the number of trees in the random forest, maximum depth of the trees and column sampling rate using a 10-fold cross-validation strategy. We used the distributed random forest function, for implementing random forest models, available in *h2o* package in *R*.

Derivation of probability threshold to categorize sensitivity and resistance

Though there is no clear relationship between the proportion of data to be used for training, testing and the model performance, Shabin et al. identified that the best results were obtained when 75% of the whole dataset was used for training and 25% for testing (9). Similar as implemented by Pfeiffer et al. and Hake et al., we used that probability cutoff as the optimal threshold to distinguish between resistant and sensitive viral sequences (10, 11). In particular, we chose for each bNAb classifier a cutoff that provided the best balance between average true positive and true negative rate.

Epitope and paratope buried surface area calculations

The buried surface area between antibody and antigen was calculated using NACCESS software (12, 13). The epitope and paratope residues for each antibody were defined as residues with

non-zero buried surface area. In the case of 2G12, the epitope residues were defined as glycans N295, N332, N339, N386, and N392, based on Scanlan et al. (14). The final epitope residues for each category were defined as follows. V1V2 category epitope residues comprised all alignment positions between residue numbers 131-196 (HXB2 numbering). The epitope residues for all other categories were defined as the union of all bNAb epitope residues within each category determined as described above.

Statistical analyses

P-value and odds ratio values presented in Fig.1c and 1d were calculated using Fisher's exact test (*R* function *fisher.test*). Statistical significance, presented in Supplementary Fig. S3 was determined using the following procedure. First, we tested for the list of AUC values for normal distribution using *R* library *nortest*, in particular function *ad.test*. If normal distribution and additionally variance homogeneity were given (*R* function *var.test*), we used t-test to determine significance (*R* function *t.test*). If neither normal distribution nor variance homogeneity were given, we applied Mann-Whitney test (*R* function *wilcox.test*).

Data and software availability

We provide all neutralization and sequence data, as well as the resistance predictors for 33 broadly neutralizing HIV-1 antibodies at https://github.com/RedaRawi/bNAb-ReP.

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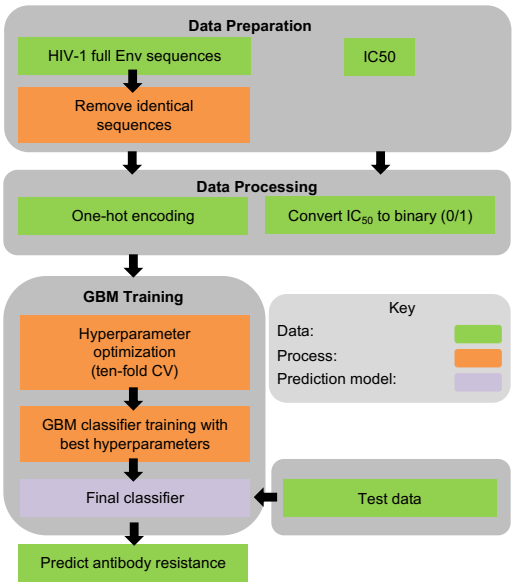

Figure S1. bNAb-ReP development flowchart

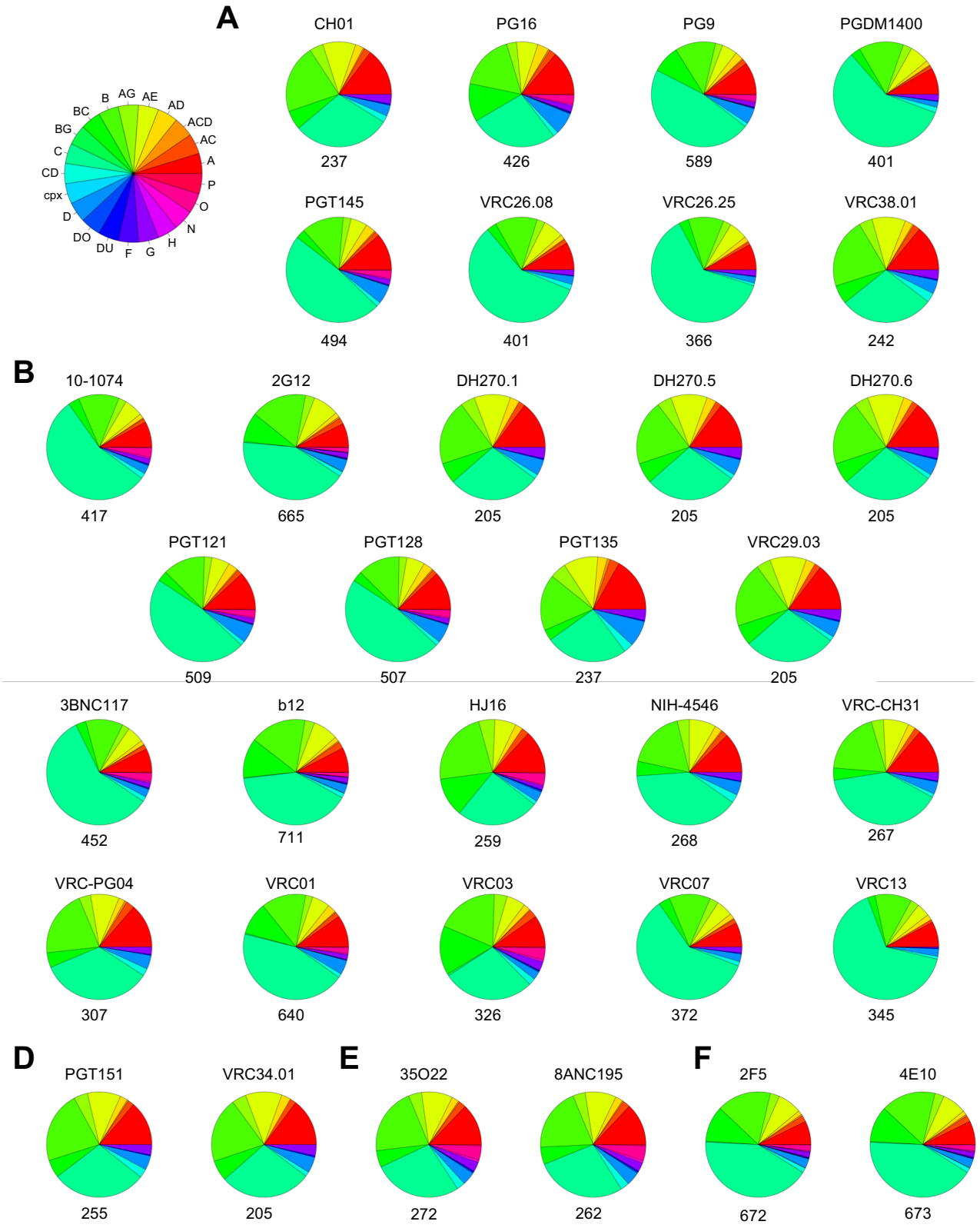

Figure S2. Training sets clade distributions
Clade distributions for each bNAb training set are illustrated as pie charts, with distinct epitope categories shown in (**A**) V1V2, (**B**) Glycan-V3, (**C**) CD4-binding site, (**D**) fusion peptide, (**E**) subunit interface, and (**F**) MPER. The number of strains within each training sets is depicted below the corresponding pie chart.

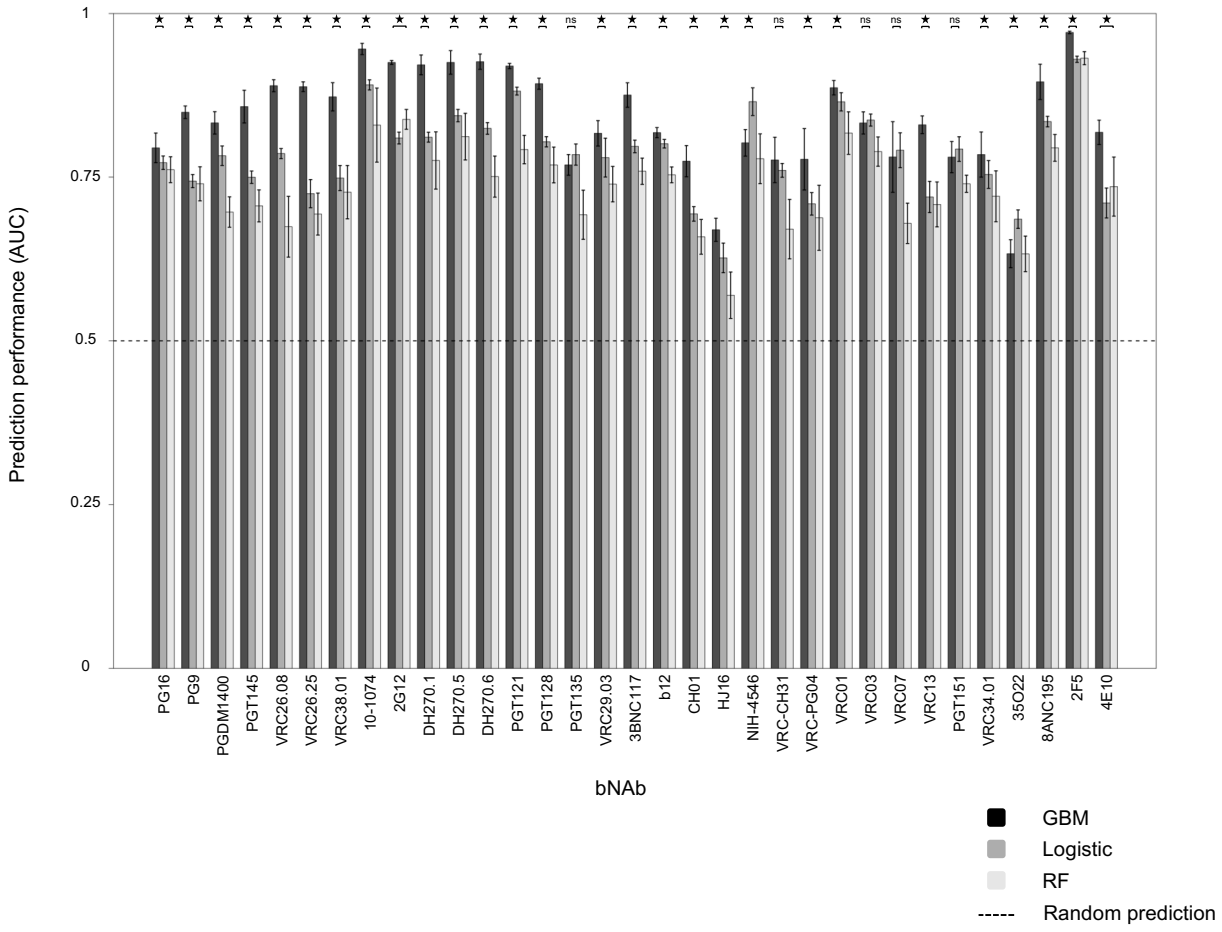

Figure S3. Prediction performance of GBM classifiers compared to Logistic Regression and Random Forest predictors.

Prediction performance (AUC) comparison of GBM (black bars), logistic regression (dark gray), and random forest (light gray) of 33 bNAb prediction models determined by ten runs of ten-fold cross-validation. For the sake of clarity, results from statistical significance testing are shown only for the top 2 models (*P-value < 0.05, ns = not significant).

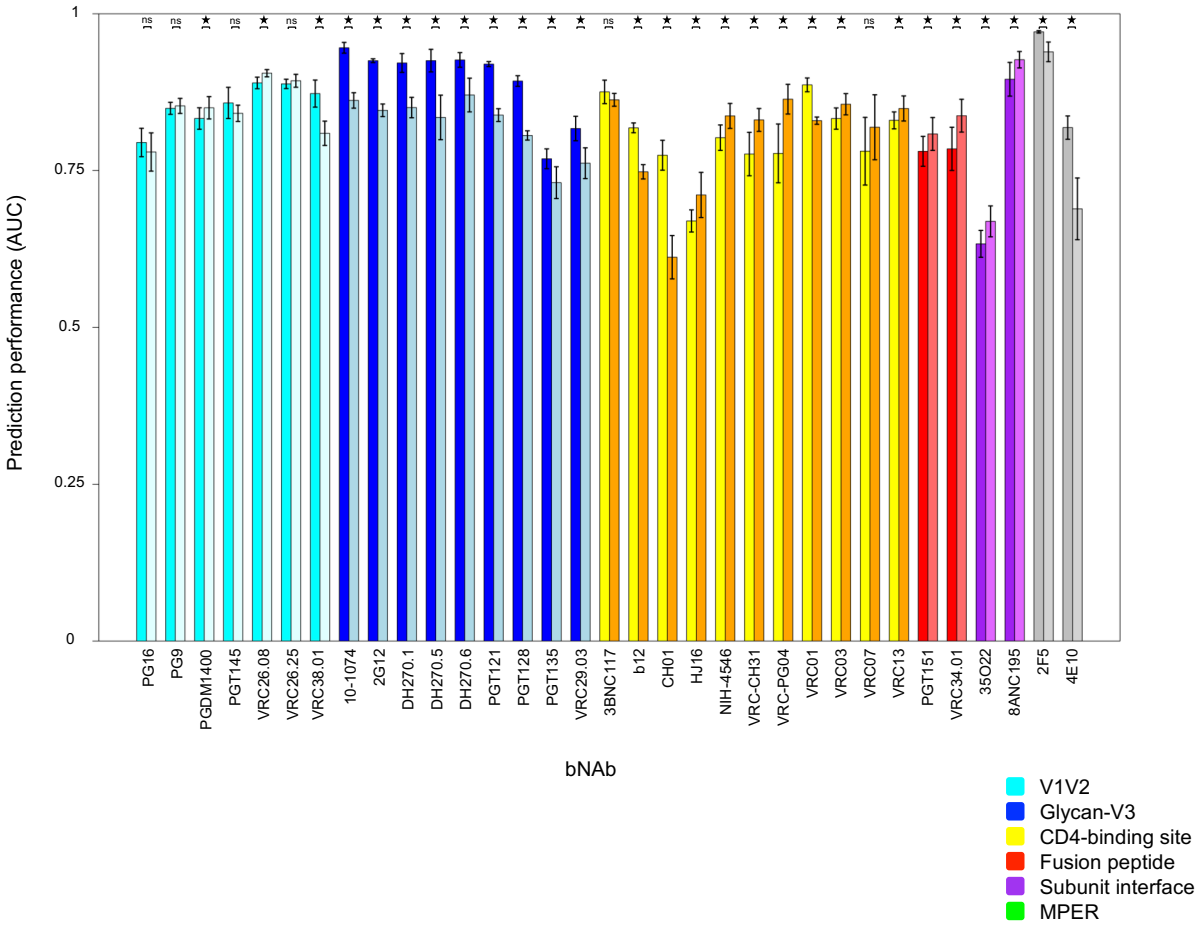

Figure S4. Prediction performance of bNAb classifiers using sequences comprising the full Env sequences or the epitope region only.

The prediction performance of the bNAb classifiers using full Env sequences or sequence subsets comprising epitope region only were determined by ten runs of ten-fold cross-validation and are shown as bar plots. The 33 different classifiers are shown on the x-axis, named according to the antibody they are trained on. The colors of the bars refer to the epitope category of the corresponding antibody. The left bar of each pair of bars refers to classifiers trained using full Env sequences, while the right bar refers to classifiers trained using epitope sequence subsets only.

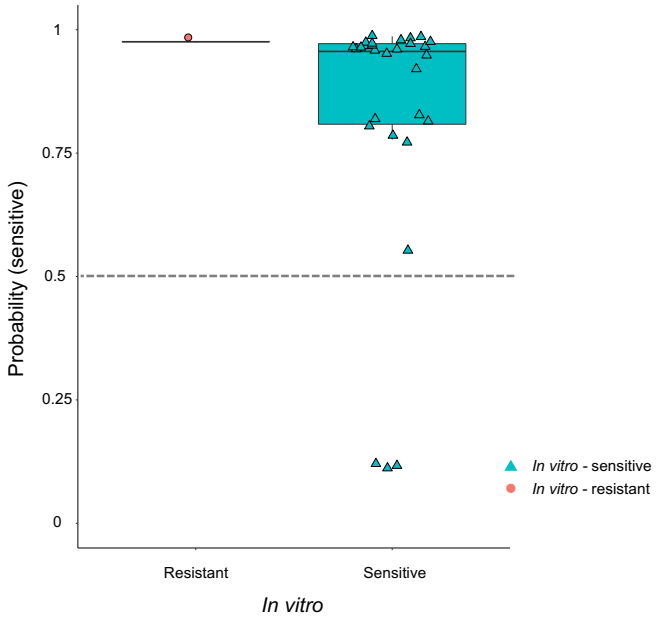

Figure S5. Prediction performance of bNAb-ReP on Env strains from bNAb 3BNC117 treatment study.
Prediction performance on bNAb 3BNC117 neutralization and sequence data shown as boxplot. *In vitro* assay neutralization classification is shown on the x-axis, with the *in silico* predicted probability for a sequence to be sensitive to 3BNC117 shown on the y-axis. The classification cutoff of 0.5 is depicted with a grey dashed line.

Supplementary Table S1. Feature importance of VRC01 bNAb classifier.

Feature	Feature importance (%)
459_G	11.13942319
456_R	9.020715034
414A_I	4.67957789
365_S	3.546548512
280_N	2.536531598
364_S	2.365870823
588_Q	2.14043756
279_D	2.035677891
364_H	1.916603082
674_S	1.534500111
354_glycan	1.429238443
839_G	1.410028298
106_T	1.382022626
269_E	1.290639271
396_L	1.185334014
274_F	1.112816848
602_V	1.094038602
413_T	1.089430625
853_A	1.082057062
389_L	0.9695362
50_T	0.960758772
400K_glycan	0.862578797
335_R	0.842405863
720_L	0.792839621
655_N	0.774759909
399_N	0.714119092
804_V	0.681868304
340_D	0.669255526
639_S	0.600308988
458_G	0.599933891
316_A	0.59664073
362_A	0.580764573
740_R	0.579182655
534_S	0.570918655
723_S	0.549697325
340_N	0.533061329
525_V	0.51898338
856_Q	0.503857971
300_S	0.490333598
293_S	0.474870562

624_G	0.47324293
155_R	0.460370358
155_K	0.452165454
152_K	0.423181955
141_V	0.411366487
683_R	0.404268098
21_I	0.401669732
343_Q	0.392644704
170_K	0.384519289
149_N	0.377551073
363_Q	0.373131642
192_R	0.372788451
49_V	0.371647651
851_F	0.354052754
703_S	0.353896049
444_K	0.353060438
403_W	0.348413332
730_P	0.336303169
348_R	0.334263924
429_E	0.332315171
316_T	0.332273048
275_K	0.330022143
279_E	0.327490564
139_T	0.323365064
417_P	0.320237403
276_glycan	0.317615543
471_I	0.314092774
272_I	0.310906952
332_K	0.310489199
607_N	0.306429062
20_M	0.291312405
63_T	0.288501722
283_T	0.288217372
787D_K	0.272161993
151_M	0.26622777
279_N	0.265424596
154_M	0.262545237
16_K	0.253780916
812_I	0.253069063
335_K	0.252709111
114_Q	0.250375426
641_T	0.248055526
730_L	0.247050741

567_K	0.245379456
320_T	0.245378522
281_A	0.244095887
173_F	0.243904663
396_N	0.23971397
132_G	0.237710795
778_A	0.231182508
63_R	0.228742164
833_G	0.2238988
461_glycan	0.219728075
333_V	0.214272549
209_T	0.213808467
80_N	0.212137819
4_K	0.210077905
144K_T	0.210043578
133_glycan	0.202913049
86_L	0.199273638
463_E	0.198643696
334_glycan	0.195780119
336_G	0.191155998
31_A	0.190776312
350_A	0.190083874
630_Q	0.185746992
130_N	0.183128064
31_T	0.181530723
535_I	0.179246405
492_K	0.178711947
138_N	0.174255959
400C_W	0.173352564
33_K	0.155484298
362_T	0.154288725
674_D	0.152903575
394_glycan	0.149147735
141_A	0.145953436
375_S	0.140886931
373_R	0.139945948
519_F	0.138839296
769_R	0.136743099
169_R	0.133736679
412_S	0.132141771
798_S	0.131442345
186i_S	0.129983813
190_E	0.12972165

62_D	0.128477198
525_A	0.127908519
624_D	0.127032909
186C_T	0.126556146
809_N	0.125197771
8_W	0.124736982
356_glycan	0.124495966
173_S	0.119938428
624_N	0.118608646
236_T	0.118136089
232_K	0.11357272
393_K	0.113443131
617_K	0.113246671
270_I	0.112952847
308_S	0.107290494
471_G	0.107203581
130_glycan	0.106226507
144B_glycan	0.106054614
702_F	0.105736095
143_A	0.104513555
4_M	0.10422366
411_glycan	0.10374832
144J_A	0.102280728
85_I	0.099610797
4_R	0.097960213
800_V	0.095582969
641_I	0.092056504
746_V	0.089771612
297_I	0.08609011
352_L	0.085986627
389_G	0.085952406
50_A	0.085911514
460_glycan	0.08517518
805_Q	0.085106445
616_glycan	0.084303261
179_Q	0.083988168
171_K	0.083293309
106_E	0.083056525
352_Y	0.082507533
731_G	0.081395469
336_D	0.081366935
565_L	0.079195127
144C_T	0.075878939

170_Q	0.075170581
446_glycan	0.074719409
731_E	0.074489848
577_Q	0.074425197
416_I	0.074369649
156_glycan	0.074173757
144_G	0.074139514
779_V	0.074105022
133_D	0.073988497
187_D	0.071946416
305_K	0.071833491
750_S	0.071323048
774_L	0.071266193
135_K	0.071196199
442_I	0.07108891
360_glycan	0.069722006
295_V	0.068672581
5_G	0.06858452
704_V	0.068197915
621_D	0.067989108
651_N	0.067464846
322_D	0.065793816
841_C	0.065441533
358_K	0.065424916
856_L	0.064983202
185_N	0.064409255
455_V	0.064171946
163_T	0.064161659
290_E	0.06246662
344_K	0.061986575
231_E	0.061908918
321_G	0.061648439
475_M	0.061066626
320_N	0.061035246
144A_S	0.060729462
146_D	0.060672761
281_V	0.060072728
705_I	0.058930696
462_S	0.058761735
289_glycan	0.058516449
8_P	0.058481006
202_A	0.058272305
200_A	0.058100147

519_L	0.057872625
394_T	0.057777199
142_V	0.057625024
307_I	0.056932306
337_Q	0.056519742
337_glycan	0.056450263
410_P	0.05643097
7_Y	0.056335756
18_G	0.055887203
676_T	0.055278078
442_K	0.054665326
192_I	0.054567606
448_glycan	0.054007296
142_G	0.053999453
463_glycan	0.053798537
186D_S	0.053071385
513_I	0.052428373
164_S	0.052265625
293_Y	0.05185073
84_I	0.051532291
277_I	0.050692325
9_H	0.050584616
398_N	0.050038767
68_V	0.049803147
29_N	0.048125197
185_E	0.04770822
750_N	0.047407874
325_D	0.047239789
195_N	0.046766536
322_E	0.046135781
186D_R	0.045865955
270_V	0.044871106
668_N	0.0440979
607_A	0.043994047
293_E	0.043325789
753_L	0.043285088
770_Q	0.043234614
668_S	0.043207195
618_T	0.043007703
5_E	0.040770049
821_A	0.040640462
777_G	0.040533316
340_E	0.040279438

787D_R	0.039833659
16_R	0.039211518
5B_M	0.038646184
211_D	0.037820515
756_I	0.037801195
732_R	0.037754135
136_D	0.037320003
33_N	0.036371353
690_A	0.036126926
658_K	0.035936344
169_K	0.035317706
209_S	0.034517785
63_K	0.034199306
363_P	0.032712572
351_E	0.032545602
395_I	0.031895506
754_A	0.031232184
467_T	0.0311497
619_L	0.030327124
291_P	0.030244051
440_E	0.02994854
165_L	0.028730217
158_S	0.028638126
179_S	0.028626081
395_F	0.028362373
354_P	0.028154713
60_G	0.0281164
496_I	0.027949231
173_Y	0.0279013
535_V	0.027720942
409_S	0.026881109
733_I	0.026607561
399_G	0.026596767
350_R	0.026417739
360_E	0.025972765
373_T	0.025533961
762_S	0.024962892
330_H	0.024360254
797_G	0.024260283
252_R	0.024114738
621_E	0.023685724
440_A	0.023498547
360_Q	0.023328561

655_K	0.023262186
633_K	0.022872689
350_K	0.022457011
840_I	0.021325762
779_T	0.021116096
595_L	0.021102854
295_glycan	0.01945349
612_S	0.01936026
490_E	0.018880448
553_S	0.018762269
47_E	0.018735365
288_L	0.01823848
339_glycan	0.017552792
779_A	0.016605813
831_E	0.016199103
275_E	0.016086297
459_D	0.015856236
413_glycan	0.015839875
328_E	0.015827913
181_I	0.01580502
135_V	0.015421099
717_L	0.015318584
87_G	0.015014226
231_K	0.014996012
22_L	0.014966842
500_K	0.014962445
349_Y	0.014959779
695_L	0.014810424
494_L	0.014759353
300_G	0.014561998
809_K	0.014281161
290_K	0.014210631
184_L	0.014084515
21_G	0.013939846
364_P	0.013850563
782_V	0.013478092
758_D	0.013334677
128_T	0.012830445
63_P	0.012533033
85_H	0.012183287
613_T	0.012085381
46_K	0.011844576
240_T	0.011344416

362_E	0.010791987
5A_I	0.01073679
330_Y	0.010671641
800_L	0.010142986
136_I	0.009990145
84_L	0.009567818
175_I	0.009314621
16_I	0.009238886
774_F	0.009027302
150_I	0.008914201
179_L	0.008619639
810_S	0.008455994
140_T	0.008316168
788_K	0.008231707
61_Y	0.008174783
161_T	0.008124686
767_S	0.007996554
388_T	0.007991136
142_N	0.007712182
84_M	0.007603355
85_V	0.007576291
354_H	0.007533432
46_R	0.007455503
742_K	0.007359883
19_I	0.007257145
459P_T	0.007206922
149_S	0.00714478
337_K	0.007117129
644_S	0.006813928
7_C	0.006812589
105_Q	0.006753652
462_glycan	0.006726639
507B_D	0.006724656
553_N	0.006205576
442_glycan	0.005506266
411_S	0.005368239
700_A	0.005367347
268_E	0.005346373
655_R	0.004987528
230_glycan	0.004591001
153_E	0.004570718
662_E	0.004418435
186C_glycan	0.004377783

429_G	0.004277492
295_I	0.004190532
99_D	0.004137473
762_N	0.004066218
25_L	0.004026744
171_T	0.003985033
717_F	0.003838424
345_I	0.003379397
60_V	0.003173227
132_T	0.002686051
29_L	0.002651904
787G_Q	0.00237012
410_S	0.002153881
659_D	0.002084533
82_Q	0.002025609
344_Q	0.001658325
358_glycan	0.001552825
281_T	0.001549052
300_N	0.001500181
784_L	0.00144775
240_K	0.001416826
741_D	0.001276793
149_T	0.001214967
839_A	0.001203856
26_M	0.001186211
136_R	0.001179731
776_S	0.001161185
587_L	0.00105952
659_E	0.001028506
283_N	0.001023159
414_I	0.000958059
700_G	0.000871272
61_T	0.000808637
287_Q	0.000768787
65_V	0.000671545
360_V	0.000658928
211_E	0.000557786
835_R	0.000457513
453_I	0.000428115
464_N	0.000426606
353_F	0.000404204
25_I	0.000385716
229_K	0.000357435

269_K	0.000349792
815_L	0.000348607
268_G	0.000320335
134_V	0.000319968
432_Q	0.000316453
389_Q	0.000294976
92_N	0.000293384
15_W	0.000289998
325_N	0.00025003
565_M	0.00023286
842_H	0.00023235
698_I	0.000230161
154_L	0.000210466
408_T	0.000206756
99_N	0.000201348
4_T	0.000180081
821_V	7.34E-05
336_T	6.35E-05
261_L	4.76E-05
322_G	4.21E-05
813_N	3.48E-05
851_L	2.35E-05
332_glycan	2.22E-05
395_Y	1.11E-05
386_N	4.17E-06

Supplementary Table S2. Feature importance of 8ANC195 bNAb classifier.

Feature	Feature importance (%)
234_glycan	22.88495943
234_N	13.39213185
276_glycan	12.19668815
349_L	7.762024202
236_T	4.778803674
15_W	4.39447887
236_K	3.054029751
278_T	2.653325309
567_K	2.460009546
272_V	2.40779405
443_I	1.971399969
513_I	1.7595767
632_E	1.666828959
8_Q	1.426869548
230_glycan	1.212115917
346_T	1.174123618
440_A	1.129961841
336_A	1.10929718
685_F	1.000928614
405_S	0.959278137
271_K	0.726755291
743_D	0.697478472
151_G	0.696037803
496_V	0.675314213
166_R	0.602167627
348_K	0.582416156
85_F	0.531671648
16_R	0.506053363
667_K	0.50392464
240_N	0.492548113
732_G	0.401376607
393_S	0.38705244
364_P	0.347079916
340_K	0.319151132
283_T	0.285876793
5B_Q	0.270768944
440_Q	0.269014747
46_K	0.26586422
630_Q	0.26541092
240_T	0.240219195

851_L	0.220587454
842_N	0.168745735
740_R	0.147150987
430_A	0.145863734
651_N	0.136247106
68_V	0.121859449
491_I	0.1027721
271_V	0.096919688
496_L	0.085356495
726_G	0.07429487
234_S	0.051492766
398_glycan	0.037094026
734_G	0.032201725
268_G	0.029990807
636_N	0.023519764
724_P	0.020782199
818_T	0.014454949
20_M	0.0142045
632_D	0.006849514
677_K	0.005064027
442_glycan	0.001793042
837_C	0.001338458
182_V	0.000363412
787C_L	0.000245629

Supplementary Table S3. Overlap of residue position with a feature importance of at least 5% (structurally determined epitope positions are highlighted in red).

bNAb	Number of features	Number of features (epitope residues)	Residue positions
b12	1	0	185
4E10	2	1	674, 787B
2F5	4	3	492, 665, 665, 667
2G12	3	2	295, 332, 395
VRC01	2	2	456, 459
PG9	2	2	160, 169
PGT128	3	1	332, 334, 334
PGT145	2	2	160, 169
3BNC117	4	2	456, 459, 466, 723
PG16	1	1	160
10-1074	3	1	332, 334, 334
VRC13	3	2	179, 471, 471
VRC03	0	0	
VRC-PG04	7	7	276, 364, 365, 389, 429, 456, 459
35O22	0	0	
NIH45-46	3	2	279, 364, 456
VRC-CH31	2	2	276, 459
8ANC195	4	3	234, 234, 276, 349
HJ16	1	1	471
PGT151	5	2	514, 519, 602, 629, 651
VRC38.01	2	2	130, 171
PGT135	4	1	179, 332, 334, 592
VRC34.01	1	1	518

Supplementary Table S4: Neutralization data of VRC01-ATI study

Assay - Luc/TZM-bl
Values are in µg/ml

Virus ID	VRC01 (IC50)	VRC01 (IC80)	3BNC117 (IC50)	3BNC117 (IC80)	10-1074 (IC50)	10-1074 (IC80)	PGT121 (IC50)	PGT121 (IC80)
V08DA POVIp - 2H3	0.293	0.982	0.213	0.937	0.016	0.075	0.011	0.047
V08DA PRAp - 2G2	0.049	0.143	0.05	0.16	0.044	0.125	0.022	0.074
V08DA POVIp - 1H8	0.203	0.602	0.198	0.618	0.019	0.064	0.006	0.021
V08DA PRAp - 2G9	0.174	0.659	0.188	0.684	0.038	0.127	0.017	0.066
V08DA POVIp - 1E4	0.192	0.643	0.263	0.916	0.036	0.127	0.019	0.072
V08DA POVIp - 2C7	0.239	1.01	0.342	1.105	0.049	0.136	0.026	0.086
V08DA PRAp - '2E12	0.359	1.23	0.41	1.535	0.05	0.165	0.031	0.119
V08DA POVIp - 2D12	0.154	0.581	0.238	0.76	0.013	0.046	0.009	0.03
V08DA PRAp - 2A5	0.25	0.766	0.399	1.154	0.045	0.121	0.027	0.084
V06 MO POVIp - 2D8	0.131	0.528	0.053	0.208	0.098	0.357	0.048	0.315
V06 MO PRAp - 1G3	1.233	4.057	0.365	1.147	0.072	0.202	0.037	0.122
V06 MO POVIp - 1F2	0.778	3.137	0.282	1.007	0.07	0.216	0.079	0.393
V06 MO PRAp - 1E2	0.634	2.32	0.227	0.826	0.09	0.297	0.043	0.194
V04EB PRAp - 1H5	2.9	8.877	3.777	11.167	1.346	6.313	>50	>50
V04EB POVIp - 2A8	3	9.52	4.233	11.567	1.46	7.817	>50	>50
V04EB POVIp - 1D1	1.96	6.39	2.1	7.275	0.568	2.865	>50	>50
V04EB POVIp - 1F8	3.56	11.95	5.485	15.7	1.079	4.915	>50	>50
V04EB POVIp - 1G4	4.033	11.167	5.295	13.25	0.937	4.71	>50	>50
V04EB PRAp - 2D9	3.09	9.38	3.57	11.7	1.466	7.125	>50	>50
V04EB PRAp - 2A10	3.47	9.795	4.775	12	1.785	7.19	>50	>50
V04EB PRAp - 2C10	3.095	9.735	3.695	11.75	1.262	7.225	>50	>50
V02RP PRAp - 2A12	0.575	2.213	0.695	3.95	0.016	0.07	0.011	0.058
V02RP POVIp - 2D4	1.575	6.41	0.606	2.245	0.031	0.101	0.02	0.066
V02RP POVIp - 1A5	1.887	6.34	0.602	2.067	0.058	0.176	0.029	0.097
V09JF PRAp - 2A11	>50	>50	3.36	10.3	0.07	0.187	0.069	0.255
V09JF POVIp - 1D4	>50	>50	2.67	7.91	0.014	0.048	0.016	0.056
V09JF PRAp - 2F9	>50	>50	4.67	12.7	0.05	0.131	0.056	0.123
V03NP POVIp - 2D5	2.565	9.74	0.282	1.175	0.237	1.012	0.261	1.17

Supplementary Data S1. HIV-1 Env sequences of VRC01-ATI study

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